



Coexistence patterns of benthic gastropods: the genus *Buccinanops* (Nassariidae) in the inner Uruguayan continental shelf and the Río de la Plata estuary

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Abstract. The analysis of the coexistence structure in assemblages of congeneric species might provide significant insights on the mechanisms underlying community assembly rules. We evaluated the existence of co-occurrence patterns among the five species of the gastropod genus *Buccinanops* occurring in the inner Uruguayan shelf and Río de la Plata estuary. Presence records were gathered from published geo-referenced data, samples from research cruises onboard R/V “*Aldebaran*” and Museo Nacional de Historia Natural de Montevideo (MNHNM). We evaluated the predictions of two species assembly hypothesis: co-occurrence due to affinity with similar conditions (niche filtering) and segregation of species due to interspecific competition (limiting similarity). After assembling a presence-absence matrix, the coexistence structure was analyzed for three spatial scales. The co-occurrence was measured using four indexes (C-score, Checkerboard distributions, Number of species combinations and V-ratio) and contrasted with two null models obtained from two resampling methods keeping columns and rows (1) fixed and (2) equiprobable. We found support to the hypothesis that coexistence of congeneric species would be less than expected by chance. However, results were dependent on the spatial scale considered and the null model used.

Keywords: co-occurrence, null models, assembly rules, benthic communities

Resumen. Patrones de coexistencia en gasterópodos bentónicos: el género *Buccinanops* (Nassariidae) en la plataforma continental interna uruguaya y estuario del Río de la Plata. El análisis de la estructura de coexistencia en conjuntos de especies congénicas puede proporcionar aportes significativos sobre los mecanismos subyacentes a las reglas de ensamble comunitario. Se evaluó la existencia de patrones de co-ocurrencia entre las cinco especies de gasterópodos del género *Buccinanops* presentes en la plataforma continental uruguaya interna y el Río de la Plata. Los registros de presencia fueron obtenidos a partir de datos geo-referenciados publicados, muestras provenientes de campañas de investigación del B/I “*Aldebarán*” y de la colección del Museo Nacional de Historia Natural de Montevideo (MNHNM). Se evaluaron las predicciones de dos hipótesis que explican el ensamblaje de las especies: la co-ocurrencia de especies debida a su afinidad por condiciones similares (filtrado ambiental) y segregación de especies debida a la competencia interespecífica (similitud limitante). La estructura de coexistencia se estudió para tres escalas espaciales a partir de la confección de matrices de presencia-ausencia. La co-ocurrencia se midió usando cuatro índices (C-score, Número de combinaciones en tablero de ajedrez, Número de combinaciones de especies y V-ratio) contrastados con dos modelos nulos obtenidos mediante dos rutinas de remuestreo: (1) manteniendo filas y columnas fijas y (2) equiprobables. Se encontró apoyo a la hipótesis de que la co-ocurrencia de especies congénicas sería menor a lo

esperado por azar. Sin embargo, los resultados dependieron de la escala espacial considerada y el modelo de remuestreo utilizado.

Palabras claves: co-ocurrencia, modelos nulos, reglas de ensamblaje, comunidades bentónicas

Introduction

The knowledge of geographic distribution of species as well as the ecological and/or historical biogeographical processes that shape these distributions is critical for the conservation and management of biodiversity. In this sense, one of the fundamental issues in ecology, and also one of the most controversial, is whether natural communities are structured according to a set of general assembly rules (Weiher & Keddy 1999).

The assembly rules could be restricting the number of possible species combinations assembled in local communities from the regional species pool. Historically, inter-specific interactions, especially competition, have been postulated as the principal structuring force in natural communities (Gotelli & McCabe 2002). However, it is also possible that pure stochastic processes, as ecological drift, are able to generate non random distributions (Ulrich 2004).

Diamond (1975) established a set of fundamental rules that determines the co-occurrence patterns of species in natural communities based on the study of avifauna in New Guinea Islands. These rules include forbidden species combinations, checkerboard distributions and incidence functions. The observed patterns were originally attributed by Diamond to (1) inter-specific competition for resources; (2) overexploitation strategies; (3) differences among species in dispersal rates and (4) low transition probabilities between permissible combinations (Connor & Simberloff 1979). This suggested that the assemblage of natural communities could be explained by some deterministic rules. However, Connor & Simberloff (1979) demonstrated that these patterns, attributed by Diamond to inter-specific competition, can also arise in randomly assembled communities. In consequence, an important debate on mechanisms underlying the observed patterns extended during the last three decades (Connor & Simberloff 1979, Diamond & Gilpin 1982, Gilpin & Diamond 1982, Sanderson *et al.* 1998, Weiher & Keddy 1999).

At a local scale, coexistence patterns could be generated by both abiotic filters and biotic interactions, acting simultaneously (Webb *et al.* 2002). Thus, only a subgroup of the regional pool of species would be represented in local communities. The characteristics of the species occurring in local

communities are thus postulated to be determined by two main principles. The niche filtering hypothesis assumes that coexisting species are more similar than expected by chance, because environmental conditions act as a filter allowing only those species able to tolerate local conditions to survive (Zobel 1997). On the other hand, the limiting similarity principle establish that coexisting species at local communities cannot be too similar because the magnitude of inter-specific competition would arise as similarity between species increases, leading to the competitive exclusion of some species (MacArthur & Levins 1967).

Even if the universality of Diamond (1975) assembly rules has not been demonstrated, less species co-occurrence than expected by chance has been observed in most natural communities (Gotelli & McCabe 2002). However, most of those works were directed, almost exclusively, to terrestrial systems, with no empiric support to conclude that this assembly rules also apply to marine systems (but see Carranza *et al.* 2010). In this line, the analysis of coexistence structure of benthic communities can provide an important empiric support to the universality of these assembly rules. Simultaneously, the analysis of the coexistence structure of assemblages of congeneric species is particularly relevant to determine which mechanism (niche filtering or limiting similarity) is the main force driving community structure: a segregated co-occurrence pattern may suggest that limiting similarity could be operating, while niche filtering could originate aggregated co-occurrence patterns. However, the distribution patterns of organisms and the processes that generate them are dependent of the spatial scale considered. At large scales, spatial heterogeneity can lead to a higher chance of co-occurrence of similar species that otherwise (i.e in an homogeneous environment) could not coexist. It follows that is likely that species with similar attributes could be aggregated at large spatial scales and segregated at small spatial scales (Webb *et al.* 2002).

Thus, the results of any ecological analysis will depend on the spatial and temporal scales considered (Wiens *et al.* 1986, Wiens 1989). This aspect has been briefly studied in relationship to assembly rules in communities, with most of the studies considering a unique spatial scale. In

Uruguay, the scale dependence phenomenon has been shown in many ecological studies of benthic invertebrates (Defeo 1993, 1996, Defeo & de Álava 1995, Giménez & Yannicelli 2000, Giménez *et al.* 2006, Giménez *et al.* 2005).

In this vein, the aims of this study are: 1) to analyze the coexistence structure in the assemblage of the benthic gastropod genus *Buccinanops* in the inner Uruguayan continental shelf and Río de la Plata estuary and 2) to examine the scale-dependence of observed patterns. We propose the following hypothesis: a) congeneric benthic species presents similar attributes. Thus, segregated co-occurrence is expected under limiting similarity while aggregated co-occurrence is expected under niche filtering and b) scale affects the observed coexistence structure of the assembly. At larger spatial scales, the likelihood of detecting aggregated co-occurrence will increase. However, a refinement of scale will generate segregation between species.

Materials and methods

Study area

The Uruguayan shelf is characterized by a dynamic hydrographic system composed of water masses of contrasting thermohaline characteristics. Subantarctic, Tropical, Subtropical and Coastal waters (mainly a mixture of Subantarctic and Río de la Plata estuary waters) are present at the study area. The occurrence of these water masses over the shelf determines a complex horizontal and vertical structure with a high degree of seasonal and interannual variation that affects the biological productivity and the dynamics of the shelf ecosystem (Guerrero & Piola 1997, Ortega & Martínez 2007). Soft bottoms formed by sand, mud and/or a mixture of both types of sediments (depending on the proximity to the estuary and the shelf topography) dominate the study area (Correia *et al.* 1996).

Study model

The gastropod genus *Buccinanops* (Nassariidae) is endemic of Southwestern Atlantic and is particularly diverse in Uruguayan waters, being distributed in a wide variety of soft bottoms. This genus is constituted by six species, five of which have been recorded in the study area (Allmon 1990, Pastorino 1993, Scarabino 2004, Scarabino *et al.* 2006). For specific nomenclature we followed Scarabino (2004) and Scarabino *et al.* (2006).

Buccinanops deformis (King & Broderip, 1832) is frequent in sandy and muddy bottoms of the Río de la Plata in front of Montevideo and Canelones. The species *B. globulosus* (Kiener, 1834)

is probably a marine and/or sandy bottoms ecotype of *B. deformis* (Scarabino *et al.* 2006) so they will be considered as the same species in this work. *Buccinanops cochlidium* (Dillwyn, 1817), type species of the genus, inhabits mainly muddy and sandy Atlantic bottoms in a depth range of 5-70 m although there are some estuarine records (Scarabino *et al.* 2006, Carranza *et al.* 2008). *Buccinanops duartei* Klappenbach, 1961 inhabits the surf zone of atlantic sandy beaches migrating closer to the swash zone during summer months (Scarabino *et al.* 2006). *Buccinanops monilifer* (Kiener, 1834) and *Buccinanops uruguayensis* (Pilsbry, 1897) are associated to sandy bottoms mainly between 10-25m depth in the Atlantic coast, but both species have been also recorded in shallow protected areas (Scarabino *et al.* 2006).

Species of *Buccinanops* are highly homogenous in their reproductive traits. All species have a complete intracapsular development (direct development), without a pelagic phase. During the embryonic development, the embryos feed on extraembryonic nourishing substances in nurse eggs. Hatching takes place in a crawling stage and hatchling size is dependent on food availability during the intracapsular stage (Penchaszadeh 1971a, Penchaszadeh 1971b, Averbuj & Penchaszadeh 2009).

The Nassariidae have been defined as typical scavengers containing some exceptions, as is the "Bullia group" (*Bullia*, *Dorsanum* and *Buccinanops*) (Brown 1982). At least one species of the closely related genus *Bullia* is known to be primary scavenger but also having predatory behaviour (Brown *et al.* 1989 and references therein, Odendaal *et al.* 1992). Trophic aspects of *Buccinanops* are largely unknown and the scarce data often comes from anecdotic, unpublished, cryptic or non-documented sources. All species are carnivores (e. g. Penchaszadeh 1971a, Escofet *et al.* 1979, Scarabino 1984, Gianuca 1983, Narvarte 2006; Estrades *et al.* 2007) but to which extent each species is a predator and/or scavenger needs to be assessed and documented more explicitly and experimentally. Scavenging behaviour have been observed and hypothesized for *B. deformis* (Narvarte 2006, Estrades *et al.* 2007, FS, pers.obs.) but predatory behaviour has been reported for *B. duartei* (Gianuca 1983).

Data gathering

The database for the assembly of a presence-absence matrix was obtained from geo-referenced published data, samples collected in research cruises of the R/V "Aldebaran" of Dirección Nacional de

Recursos Acuáticos (DINARA) and information from specimens stored in the Museo Nacional de Historia Natural de Montevideo (MNHNM) malacological collection. The determination of species for all specimens was directly verified by a taxonomist. Only live-collected individuals (preserving opercula and/or periostracum in good conditions) were considered, damaged and sub-fossil shells being excluded. The congruence of spatial data was also verified, considering only those records referred to precise locations.

Data were organized as a presence-absence matrix, where each row represents a species and each column represents a site. The entries of the matrix indicate the presence (1) or absence (0) for each species in a particular site (Connor & Simberloff 1979). For the evaluation of scale dependence, we constructed matrices using square cells whose sides measured 0.10° , 0.25° and 0.50° .

Co-occurrence indexes

We used four indexes that describe through a single value, the co-occurrence structure of the presence-absence matrix:

(1) The number of checkerboard species pairs (Checker) (Diamond 1975). This index measures the number of species pairs that never co-occur. In a competitively structured community, there should be more checkerboard pairs of species than expected by chance.

(2) The C-score (Stone and Roberts 1990) measures the average number of "checkerboard units" between all possible pairs of species. The number of checkerboard units (CU) for each species pair is calculated as:

$$CU = (r_i - S)(r_j - S)$$

where S is the number of shared sites (sites containing both species) and r_i and r_j are the row totals for species i and j . The C-score is the average of all possible checkerboard pairs, calculated for species that occur at least once in the matrix. Thus, the C-score measures segregation between species, but unlike the Checker it does not require perfect checkerboard distributions. In a competitively structured community, the C-score should be significantly larger than expected by chance.

(3) The number of species combinations (Combo) (Pielou & Pielou 1968). This index measures unique species combinations represented in different sites. Thus, in a competitively structured community, there should be less species combinations than expected by chance.

(4) The variance ratio (Robson 1972, Schluter 1984). The V-ratio is calculated as the ratio of the variance in species richness to the sum of the variance in species occurrence. If the species are

distributed independently and the sites are equiprobable, the expected value of the ratio is 1.0. If there is strong negative covariance between species pairs, the variance ratio will be < 1.0 and if there is positive covariance between species pairs, the variance ratio will be > 1.0 . This index measures the variability in species richness per site. Thus, in a competitively structured community, the observed variance ratio should be significantly smaller than expected by chance.

Of the four indexes, the C-score is not prone to type I and II errors (false positives and negatives respectively) (Gotelli 2000). Thus, it easily detects species pairs that do not co-occur frequently. The C-score and the V-ratio are based on the average co-occurrence and covariance, respectively, of all species pairs. Therefore, minor changes of the data do not affect these indexes.

However, the number of checkerboards and the number of species combinations may cause the null hypothesis to be incorrectly accepted because a change in a single species occurrence can create or destroy a perfect checkerboard, or add or delete a species combination.

Null models

The statistic significance of the four co-occurrence indexes for the three spatial scales was evaluated using two null models generated by two different resampling methods: (1) keeping columns and rows fixed (Sim I) in order to maintain richness per site and number of occurrences of each species as in the original data set and (2) with columns and rows equiprobable (Sim II). Here, every site and species is equally likely to be represented in random matrices. The V-ratio index is exclusively determined by row and columns totals of the matrix, so in the Sim I no changes in the index will be observed, even if all simulated matrices differ from the original.

For each analysis, 5000 null matrices were generated using a sequential swap algorithm. In this algorithm the initial point is the original matrix, and certain elements of the matrix are repetitively swapped in order to achieve a random matrix. This algorithm has been extensively evaluated showing good statistical properties (Gotelli & Entsminger 2003). The co-occurrence analysis were developed using the simulation software EcoSim 7.0 (Gotelli & Entsminger 2001).

Both null models were used because uncertainty about the quality of the sampling. If we assume a scenario where sites were exhaustively sampled it is reasonably to maintain richness and occurrence of the original data set in the null community. However, in a scenario where sampling

would be incomplete it is more convenient not to establish that restrictions and assume that all sites are equivalent.

Finally, we analyzed the internal structure of coexistence for all possible species pairs in the three scales considered. We constructed a CU frequency distribution histogram adjusted to a normal distribution using the Kolmogorov-Smirnov test.

Standardized effect size

In order to compare the different indexes and scales, we calculated a standardized effect size (SES), analogous to the SES that is used in meta-analysis (Gurevitch *et al.* 1992). This index measures the number of standard deviations that the observed index is above or below the mean of the simulated communities as:

$$SES = (I_{obs} - I_{sim}) / \sigma_{sim}$$

where I_{obs} is the observed index, I_{sim} is the simulated index and σ_{sim} is the standard deviation of the simulated indexes. It scales the results in units of standard deviations, which allows for meaningful

comparisons among different tests. A standardized effect size that is greater than 2 or less than -2 is statistically significant with a tail probability of less than 0.05 (Gotelli & McCabe 2002).

Results

Database and distribution maps

We obtained a database with 210 presence entries of the five species of *Buccinanops* for the inner Uruguayan continental shelf and Río de la Plata estuary. The species showed congruent distributions with those published by Scarabino *et al.* (2006). The presence records of *B. cochlidium* were obtained for a wide range of depths for the Atlantic ocean and Río de la Plata (Fig. 1a). *Buccinanops duartei* (Fig. 1c), *B. monilifer* (Fig. 1d) and *B. uruguayensis* (Fig. 1e) distribution is mainly Atlantic, but unlike *B. cochlidium* these species are distributed in shallower areas. *Buccinanops deformis* showed an estuarine distribution (Fig. 1b).

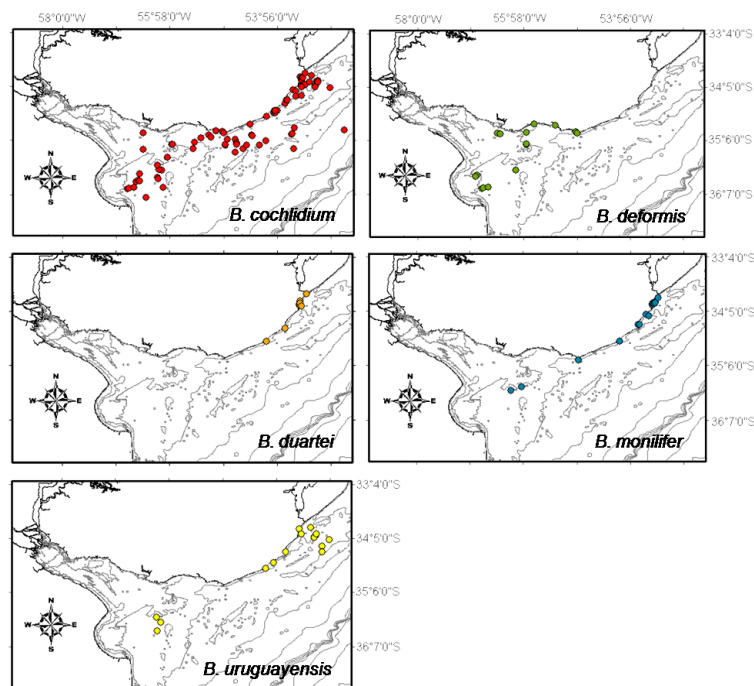


Figure 1. Distribution of the five species of *Buccinanops* in the inner Uruguayan continental shelf, based on published geo-referenced data, samples collected at oceanographic cruises of the R/V “Aldebaran” and data from the malacological collection stored at Museo Nacional de Historia Natural de Montevideo (MNHNM).

Co-occurrence analysis

The results from co-occurrence analysis are resumed in Table I. Results from the application of the Sim I showed, in general, a good consistence with the predictions formulated for the small spatial scale where we observed a segregation pattern between species (0.10, Checker and Combo).

However, we found no consistent results with the hypothesis of an aggregation pattern at the largest scale. On the contrary, 2/3 of the results indicated that the gastropods association is probably structured by competition (0.50, C-score and Combo).

The results derived from Sim II differed widely from those obtained from Sim I. At a small

spatial scale we found that 2/4 of the results indicated a segregated distribution of species (0.10, Checker and Combo) while the other two suggested the aggregation of the species thus, rejecting the hypothesis of segregation due to competition processes at small spatial scales. The same response was observed for the intermediate scale. At the large scale 2/4 of the results indicated an aggregated

pattern (0.50, C-score and V-ratio) while only one suggested a segregated distribution (Combo).

In Table II the number of Checker units (CU) for each species pair of the original matrix is showed. The species pairs with a higher number of CU showed less co-occurrence than those with fewer units.

Table I. Co-occurrence indexes results for the null models applied: columns and rows fixed (Sim I) and columns and rows equiprobable (Sim II), for cells of 0.10°, 0.25° and 0.50° of side. For each simulation and resampling method the observed co-occurrence value and the average of the simulated indexes are shown (in bold). Statistically significant results ($p < 0.05$). Checker: number of checkerboard distributions; Combo: number of species combinations; n.s: not significant.

	NULL MODEL SIM I	NULL MODEL SIM II
CELL 0.10° OF SIZE		
C- score	79,50 (80,20 ; $p = 0.47$)	79,50 (146,86 ; $p = 0$)*
Checker	2,00 (0,30 ; $p = 0.01$)*	2,00 (0,20 ; $p = 0.02$)*
Combo	11,00 (13,64 ; $p = 0.02$)*	11,00 (26,82 ; $p = 0$)*
V-ratio	-	1,09 (0,61 ; $p = 0$)*
CELL 0.25° OF SIZE		
C- score	50,30 (48,73 ; $p = 0.23$)	50,30 (93,56 ; $p = 0$)*
Checker	1,00 (0,22 ; $p = 0.21$)	1,00 (0,03 ; $p = 0.03$)*
Combo	12,00 (13,64 ; $p = 0.14$)	12,00 (20,35 ; $p = 0$)*
V-ratio	-	1,12 (0,67 ; $p = 0$)*
CELL 0.50° OF SIZE		
C- score	17,10 (14,37 ; $p = 0.01$)*	13,60 (22,35 ; $p = 0.02$)*
Checker	1,00 (0,14 ; $p = 0.13$)	1,00 (2,17 ; $p = 0.36$)
Combo	8,00 (11,36 ; $p = 0$)*	8,00 (18,75 ; $p = 0$)*
V-ratio	-	1,48 (0,79 ; $p = 0$)*

Scale dependency

The CU frequency distribution for every species pairs did not differ from the normal distribution for any cell size (Kolmogorov-Smirnov; $p > 0.05$ in every case). The modal average shifted right side showing an increase in the CU to smaller cell sizes. The frequency distribution flattened to smaller scales indicating a rise in the variance (Fig. 2).

Standardized effect size

The results of the standardized effect size for both simulation routines were in total concordance with results obtained from co-occurrence analysis, with different processes structuring the gastropods association depending on the co-occurrence index considered. However, the indexes response did not change, in general, with the scale in opposition with the hypothesized segregation of species at small scales and aggregation of species as we increase the spatial scale size.

Table II. Number of checkerboard units (CU) for each species pair observed in the original matrix for cells sizes of 0.10°, 0.25° and 0.50° side.

CELL 0.10° OF SIZE					
Species	<i>B. cochlidium</i>	<i>B. deformis</i>	<i>B. duartei</i>	<i>B. monilifer</i>	<i>B. uruguayensis</i>
<i>B. cochlidium</i>	x	255	53	49	88
<i>B. deformis</i>		x	55	99	140
<i>B. duartei</i>			x	5	11
<i>B. monilifer</i>				x	40
<i>B. uruguayensis</i>					x
CELL 0.25° OF SIZE					
Species	<i>B. cochlidium</i>	<i>B. deformis</i>	<i>B. duartei</i>	<i>B. monilifer</i>	<i>B. uruguayensis</i>
<i>B. cochlidium</i>	x	124	68	29	26
<i>B. deformis</i>		x	50	56	99
<i>B. duartei</i>			x	5	18
<i>B. monilifer</i>				x	28
<i>B. uruguayensis</i>					x
CELL 0.50° OF SIZE					
Species	<i>B. cochlidium</i>	<i>B. deformis</i>	<i>B. duartei</i>	<i>B. monilifer</i>	<i>B. uruguayensis</i>
<i>B. cochlidium</i>	x	42	0	0	0
<i>B. deformis</i>		x	36	35	56
<i>B. duartei</i>			x	0	0
<i>B. monilifer</i>				x	2
<i>B. uruguayensis</i>					x

Discussion

Overall, coexistence patterns were detected for *Buccinanops* species in the Uruguayan continental shelf, since the null hypothesis was rejected in most cases (71%). However, some analysis (43%) suggest less co-occurrence than expected by chance while a smaller proportion (29%) suggest a positive co-occurrence between species. Thus, in this assemblage, the limiting similarity mechanism would predominate over niche filtering. In this sense, the mutual segregation between species pairs (produced e.g. by inter-specific competition or niche displacement over evolutionary time-scales) could be important in the assemblage structure. However, the patterns observed did not change with the spatial scale considered in opposition to what was expected.

The results depended mostly on the resampling method used. When maintaining columns and rows fixed (Sim I), a higher proportion of results supported the null hypothesis of random distribution (56%). Additionally, the significant results poorly differ from random expectations when considering the SES. This model has good type I

properties so it is unlikely that the null hypothesis is rejected when it is true (Gotelli 2000). However, some authors (e.g. Alatalo 1982, Diamond & Gilpin 1982, Gilpin & Diamond 1984) proposed that the restrictions this model apply make it too conservative, so the null hypothesis is accepted more frequently than it should. Results differed from Sim II, with only a minimum proportion of results supported the null hypothesis (8%) and with results differing widely from the expected by chance when considering the SES. In this case, half of the results indicated a positive co-occurrence between species. This model presents a higher tendency to type I error. Gotelli & Ellison (2002) used two resampling methods (fixed-fixed and weighted-fixed) to determine the coexistence structure of the New England ant community and their results did not show any differences between simulations but differed for different spatial scales and environmental conditions. King (2007) using the same methodology for Florida ants obtained similar results as Gotelli & Ellison (2002). In contrast with our study, the above mentioned authors employed two conservative models.

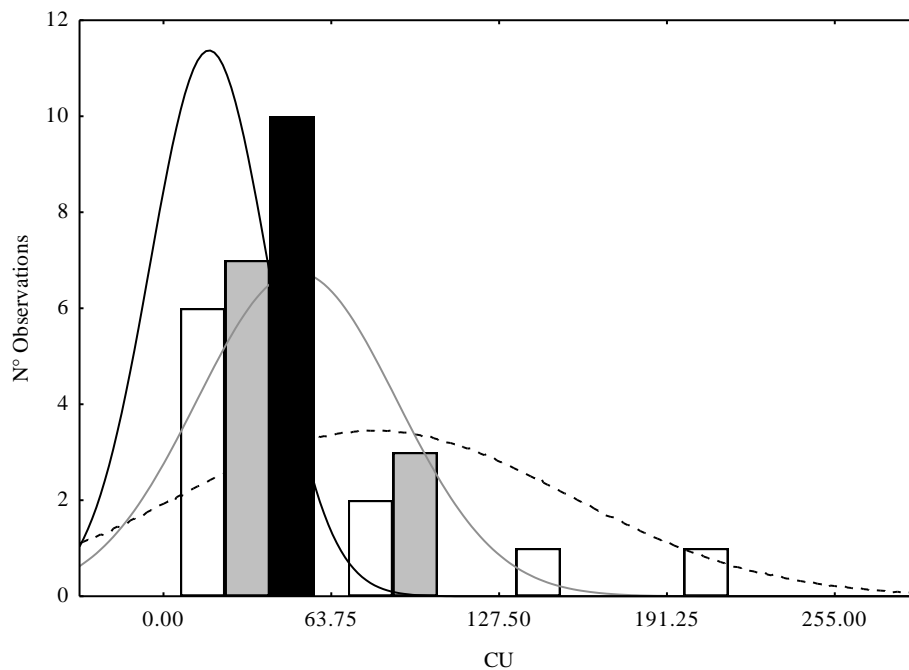


Figure 2. Frequency distribution of checkerboard units (CU) for three cell sizes: 0.10 (white); 0.25 (grey); and 0.50 (black) with their normal distributions fitted (dotted line, grey and black respectively).

Thus, if our data were resultant from an exhaustive sampling (Sim I), the *Buccinanops* assemblage would be in general random concerning coexistence between species pairs based on co-occurrence indexes. However, when we analyze results from SES, the assemblage changes from random distributed to a competition structured assemblage. Moreover, if we observe the trends of non significant results of the co-occurrence indexes the majority supports a segregated structure. On the other hand, in a more flexible scenario, with an incomplete sampling (Sim II), the presence of coexistence patterns would be predominant but it is not clear whether dominant interactions are negative or positive.

The coexistence mechanisms that operate in homogeneous and competitive environments have been mostly studied using a patch occupation approach (Levins, 1969) that records the presence and absence of species. This approach assumes that local competitive interactions are produced at a smaller temporal scale than dispersion (Cohen 1970, Levins and Culver 1971, Hastings 1980). However, the database used is not resultant of a unique sampling event, but is the result of a sum of occurrence events of species along time. Thus, the possibility to find a particular species in a sampling

unit would be higher, possibly leading to an overrepresentation of species occurrence, raising the probability of non detection of patterns.

Additionally, the observed coexistence structure of the assemblage differed between scales, being mostly random at intermediate scale, while at smaller and larger scales spatial segregation between species decrease and increase respectively. This differed from our hypothesis, where the chance of pattern detection would decrease at larger scales, suggesting a non linear behavior of the response variable (detection probability of coexistence of species patterns).

In the assemblage there are less species combinations than expected by chance (COMBO index), a tendency observed for every scale and resampling method. Thus, there are certain species combinations that do not exist in nature in agreement with Diamond (1975) assembly rules, and in congruence with Gotelli & McCabe (2002) meta analysis results. This index is, as well as the Checker, one of the most prone to type II errors, which indicates that the pattern detection in this case is robust.

In the assemblage there are species pairs distributed forming perfect checkerboards, so they do not co-occur at any site. This is in agreement with

Carranza *et al.* (2010) that detected a non-random distribution using this index for 120 species of gastropods in the Uruguayan continental shelf. Further, this index will be dependant of the scale considered, rising the detection probability of this perfect segregation as we refine the scale. At the smaller scale (0.10°) species pairs that showed this type of distribution were *B. deformis*- *B. duartei* and *B. deformis*- *B. monilifer*, species found in contrasting environments. *Buccinanops deformis* is found in estuarine subtidal environments while *B. duartei* and *B. monilifer* are commonly found in the

Atlantic coast, with previous records of *B. duartei* for the Río de la Plata (e.g. Giberto *et al.* 2004) based on misidentifications of *B. deformis*. At intermediate and larger scales, segregation between *B. deformis* and *B. duartei* is detected (Scarabino *et al.* 2006). This tendency is in agreement with the expected: as we consider larger scales, the probability of detecting segregation between species pairs becomes lower, coinciding with the intuitive interpretation of distribution maps where the more segregated species were *B. deformis* and *B. duartei*.

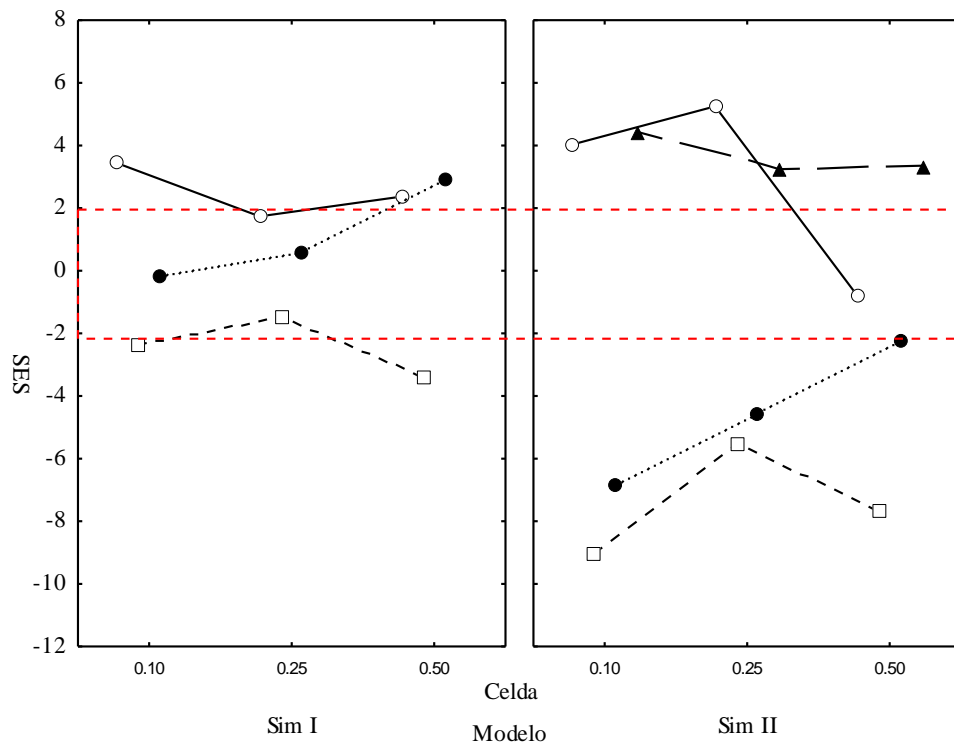


Figure 3. Standardized effect size (SES) for the co-occurrence indexes: Checker (○) V-ratio (▲) Combo (□) C-score (●) for the three cell sizes considered (0.10, 0.25 and 0.50° of side) and the two resampling methods: with columns and rows fixed (Sim I) and equiprobable (Sim II).

Even if we had found more perfect checkerboards distributions than expected, the C-score showed that species tended to co-occur more than expected by chance. In this sense, niche filtering could cause congeneric species to be found together in the same environment because they tolerate similar conditions. This results are in agreement with Simberloff (1970) who reviewed and analyzed patterns in the species/genus rate at local communities and found that the observed rate was usually higher than expected, in contrast with predictions from competition theory (Gotelli &

Colwell, 2001). This pattern is congruent for the three scales in the more flexible scenario (Sim II). However, in a less flexible scenario (Sim I) in the largest scale, an opposite trend (less co-occurrence) is observed. This index presents very good statistical properties when used with Sim I, so pattern detection in this case cannot be attributed to false positives. However, when used with Sim II it is prone to detect patterns when it does not exist.

The V-ratio indicates that the assemblage showed more co-occurrence than expected by chance, so species are not independently distributed

in equiprobable sites, and considerable heterogeneity in species richness per site can be observed. For the *Buccinanops* assemblage, the hypothesis of niche limitation of Wilson (1987) seems not be validated. The hypothesis states that species richness variance per site should be small if the number of species inside the guild is limited by competition. This tendency is observed for the three scales, being meaningful for 0.50° cells where there is a greater probability of co-occurrence. Our results are in agreements with those of Schluter (1984) who used the V-ratio as a co-occurrence index and found that the patterns present in published matrices tended to be random or slightly positive. This null model assumes that all sites are equiprobable so negative co-occurrence patterns would be hiding behind the heterogeneity between sites.

Coexistence between species could be achieved through differentiation in the biotic or abiotic environment they inhabit, through a species life history differentiation or through the interaction of both mechanisms (Amarasekare *et al.* 2004). For species of *Buccinanops*, differentiation in life history does not seem to be the explanation because of e.g. the homogeneity in reproductive traits. However, the adaptation to different types of substrata or salinity could act as a mechanism promoting patterns of coexistence in the assemblage.

From checkerboard units (CU) we observe that species pairs that, in average, co-occur less are *B. deformis* and *B. cochlidium* followed by *B. deformis* and *B. uruguayensis*. On the other hand, *B. monilifer* and *B. duartei* followed by *B. uruguayensis* and *B. duartei* showed less segregation. However, this is not congruent neither with the observed on distribution maps, nor with information available. The number of CU is not an appropriate index to measure co-occurrence between species pairs because it is dependent on the number of records. In this case, species that present a higher number of CU are those with a high number of records and thus with a greater chance to form checkerboard distributions. However, as we increase the scale, we observe an increase in the CU number. The combination of this analysis with studies of niche overlapping could help us to understand if checkerboard distributions are produced by competition or another segregating force, or simply by an artifact of the index used here.

This work constitutes the first analysis of coexistence patterns of a benthic congeneric species assemblage. In general, as we observe from the SES, the pattern detection in the assembly depends on the coexistence index, the resampling method as well as on the spatial scale considered. Thus, a multiscale

approach using different indexes is recommended for this kind of analysis.

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