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Temporal dynamics of gastropod fauna on subtidal sandy sediments of the Ensenada de Baiona (NW Iberian Peninsula)

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Abstract The temporal variation of the gastropod fauna inhabiting sandy sediments of the Ensenada de Baiona (Galicia, Spain) was studied at three subtidal sites from February 1996 to February 1997 by means of quantitative sampling. A total of 5,463 individuals representing 51 gastropod species and 22 families were found. The family Pyramidellidae was the most diverse in number of species (11 species), followed by Rissoidae and Trochidae (4 species each). The dogwhelk, *Nassarius reticulatus*, and the rissoid snail, *Rissoa parva*, were the numerically dominant species at the three studied sites; those and other abundant species showed their greatest densities by the end of summer and the beginning of autumn. In general, univariate measures of the assemblage (number of species, abundance, diversity, evenness) showed variations through time; greater values were recorded between summer and autumn depending on the site. Multivariate analyses done on abundance data showed certain seasonality in the evolution of the assemblage as expected for shallow subtidal sandy sediments at temperate latitudes; those seasonal changes were mostly related to variations in abundance of numerically dominant species. Although the measured sedimentary variables did not show significant correlations with faunal univariate parameters, sediment heterogeneity due to the presence of mats of *Zostera marina* L. and shells of dead bivalves might explain the differences in composition of the gastropod assemblage among sampling sites.

Keywords Gastropoda, sediment, subtidal, dynamics, Ensenada de Baiona, Iberian Peninsula, Atlantic Ocean

Introduction

Marine sedimentary substrata are the most common habitat in the marine environment (Snelgrove 1999) and are inhabited by a variety of benthic faunas. Distribution and composition of those faunas are conditioned by a number of abiotic factors and biotic interactions (Gray 1981). In temperate latitudes, soft-bottom benthic faunas show temporal variations in abundance of species and composition of assemblages which have been related, in turn, to seasonal changes in temperature, food supply and granulometric composition (e.g. Buchanan et al. 1974; Nichols and Thompson 1985; Dauvin and Ibanez 1986; Frid et al. 1996). The study of temporal evolution of benthic assemblages is of great interest to determine whether there are long-term changes in their structure (Josefson and Rosenberg 1988; Van Hoey et al. 2007) and to assess the scope and impact on the dynamics of benthic assemblages of the life cycles of species (Boero 1994; Constable 1999), biotic interactions (Bonsdorff and Blomqvist 1993; Turnberg and Krang 2008) and abiotic factors and anthropogenic disturbances (Zajac 1991; Underwood 1992; Pearson and Mannvik 1998; Hily et al. 2008). This information is paramount when formulating models and quantitative predictions about the functioning of natural systems in general, and of marine soft-bottom biota in particular (Constable 1999).

The Galician rias (NW Spain) are a kind of estuarine system defined as a stretch of coast characterised by the occurrence of a (paleo) valley occupied by the sea (Richthofen 1886; Evans and Prego 2003). The great variety of habitats and sediments present in the rias results in diverse benthic faunas both in hard and sedimentary substrata (e.g. Mora 1982; López-Jamar et al. 1995; Olabarria et al. 1998). Their shorelines are highly populated and thus subjected to the effects of many human activities. Indeed, the soft-bottom benthic faunas of many rias are greatly affected by mussel culture, urbanization of the shoreline, paper mill discharges and urban sewage (López-Jamar et al. 1986). The effects of these perturbations

mostly translate into organic enrichment and changes in sedimentary composition (López-Jamar 1978; López-Jamar and Mejuto 1985), which, in turn, results in changes in assemblages and affects the stability and dynamics of populations of many species.

Molluscs are an important component of benthic faunas in sandy marine sediments in terms of abundance and biomass (Cadée 1968; Troncoso and Urgorri 1993; Lourido et al. 2006; Laudien et al. 2007) and its study may provide valuable information about the state of benthic assemblages and environmental conditions (Bresler et al. 1999; Nehring 2005; Amin et al. 2009). Gastropods inhabiting subtidal soft-bottoms have a great influence on the populations of other benthic animals; for instance, naticids and retusid opisthobranchs are active predators of bivalves and turrids prey on small polychaetes (e.g. Ansell 1960; Shimek 1983; Hiddink et al. 2002). Therefore, the study of the composition and temporal variation of gastropod assemblages may help to understand the evolution and functioning of the whole benthic assemblage. Nevertheless, specific studies on temporal dynamics of gastropod assemblages on sandy soft bottoms are scarce when compared to those devoted to other components of the benthic macrofauna (Ambrose 1991; Sardá et al. 1995; Carpentier et al. 1997; Dauvin 1998); in many occasions, those are often integrated within general studies also including bivalves, polychaetes and crustaceans.

Despite the social and economic importance of the Galician rias, there are many areas whose benthic fauna is still little known, including their gastropod faunas. This is the case of the Ensenada de Baiona, which is an inlet located south of the Ría de Vigo. Subtidal sediments are mainly sandy in most of its extension and have not been subjected to human alterations apart from some areas affected by the construction of the harbour jetty during the 1970s. Previous data on gastropods of the inlet come from taxonomic studies or checklists of species such as those provided by MacAndrew (1849), Hidalgo (1886), Rolán (1983) and Rolán et al. (1989). Recently, Moreira et al. (2009) described the spatial distribution and

composition of its subtidal soft-bottom gastropod assemblages revealing the presence of a rich gastropod fauna. However, temporal dynamics of those assemblages have not been described from this area yet and have been, in general, scarcely studied in other Galician rias. In this paper, the temporal evolution of gastropod fauna on three subtidal sandy sites is described after quantitative sampling done during a one-year period; this was done to test whether there is any intra-annual trend in composition of assemblages, values of univariate measures (number of species, total abundance, diversity, evenness) and abundance of species.

Material and methods

Study area

The Ensenada de Baiona is located on the southern margin of the mouth of the Ría de Vigo, at 42°07'N–42°09'N and 08°51'W–08°49'W. The inlet is a marine environment with salinity ranging from 32‰ in winter to 35‰ in summer in the outer area, and from 28‰ to 35‰ in the harbour area. The northern and eastern margins of the inlet are limited by sandy beaches; the western outer margin is exposed to the oceanic swell and winter winds (Alejo et al. 1999). Most of the inlet soft bottoms are sandy and their distribution follows a gradient in grain size (Alejo et al. 1999; Moreira et al. 2005). Sediments at the outer mouth of the inlet are composed by very coarse to coarse sand; sedimentary substrata in the central area are dominated by medium and fine sand; sediments in the northern and eastern margins are mainly composed by fine to very fine sand fractions (Moreira et al. 2005). The harbour jetty built during the 1970s shelters the southern area around the harbour of Baiona, which has contributed to an increase of deposition of finer particles (Alejo and Vilas 1987); sediments at this area range from sandy mud to mud.

Sampling

Quantitative sampling was done at the Ensenada de Baiona in a monthly basis between February 1996 and February 1997 at three subtidal sites (Fig. 1). Sampling sites were chosen as representative of the fine-sand sediments in the inlet (Moreira et al. 2005); abiotic characteristics of the three sites are summarized in Table 1. Site D2 had scattered mats of the seagrass, *Zostera marina* (L.); site D15 was close to the largest sandy beach in the inlet (Praia América). Sites D2 and D17 had a greater qualitative presence of shells of dead molluscs (mostly bivalves) than site D15. Five replicates were taken at each site on each date using a Van Veen grab with a sampling area of 0.056 m² thus covering a total area of 0.28 m². Samples were sieved through a 0.5 mm mesh and fixed in 10% buffered formalin for later sorting and identification of the fauna. An additional sediment sample was taken at each site to determine granulometric composition, grain-size median (Q₅₀), sorting coefficient (S_o) and total organic matter (TOM, %). The following sedimentary fractions were considered: gravel (>2 mm), very coarse sand (2–1 mm), coarse sand (1–0.5 mm), medium sand (0.5–0.25 mm), fine sand (0.25–0.125 mm), very fine sand (0.125–0.063 mm), and silt/clay (<0.063 mm). The total organic matter content was estimated from the weight loss on combustion at 450°C for 4 hours (Buchanan 1984).

Data analyses

The following univariate parameters were calculated for each date and sampling site: total abundance (N), number of species (S), Shannon-Wiener diversity index (H', log₂) and Pielou's evenness (J'). For each site, a one-factor ANOVA (Analysis of Variance) was used to test whether those parameters showed significant differences among sampling dates; the homogeneity of variances was previously evaluated by means of Cochran's C test. Where ANOVA showed significant differences ($P < 0.05$), a post hoc Student-Newman-Keuls (SNK) test was then done for *a posteriori* comparisons of the means from each sampling date.

Multivariate analyses were done through the PRIMER 6 software package (Clarke and Gorley 2006). A similarity matrix between samples was constructed by means of the Bray-Curtis similarity index by first applying square root transformation on species abundance to downweight the contribution of the most abundant species. Data were previously averaged through the five replicates for each date and site thus obtaining a centroid. From the similarity matrix, a classification of the samples was done by cluster analysis based on the group-average sorting algorithm, obtaining a dendrogram. Clusters of samples determined as statistically significant by profile test SIMPROF ($P < 0.05$) were considered as having a similar gastropod composition. Non-metric multidimensional scaling (nMDS) was used to produce a visual representation of the ordination of centroids. Analyses of correlation among univariate parameters and granulometric features were done by means of the Spearman's correlation coefficient. The possible relationship between gastropod fauna and the measured sedimentary variables was explored using the BIO-ENV procedure (PRIMER). All variables expressed in percentages were previously transformed by $\log(x+1)$.

Results

Faunal composition

A total of 5,463 individuals representing 51 gastropod species belonging to 22 families were identified in samples. The family Pyramidellidae was the most diverse being represented by 11 species, followed by Rissoidae and Trochidae (4 species each). The gastropod fauna present at site D15 was, in general, poorer in terms of number of individuals and species than those at the other two sites (Table 1). Sites D2 and D17 showed a similar total number of individuals; site D17 was the richest in number of species. The gastropod assemblage was numerically dominated at the three sites by the dogwhelk, *Nassarius reticulatus* (Linnaeus, 1758), and the rissoid snail, *Rissoa parva* (da Costa, 1778), which both accounted for between

37% and 89% of total abundance at any given site; the calyptraeid, *Calyptraea chinensis* (Linnaeus, 1758), and the turritellid, *Turritella communis* Risso, 1826, were also abundant at site D17. At sites D2 and D17, about half of the species found were represented by less than 10 individuals in total; at site D15, all species but *N. reticulatus*, *R. parva* and the turrid, *Bela nebula* (Montagu, 1803), were found in small numbers (less than 3 individuals in total each).

For all sites, half of the species were present at least in more than 50% of samples (6 or more months). Ten species were shared by the three sites, of which most of them were numerically dominant (>1% of total dominance). Seventeen species out of the 51 found were only present in site D17, 6 were exclusive of site D2 and 5 were only found at site D15; most of these species were collected in low numbers and were present, in general, in a few monthly samples apart from *T. communis* and *Mangelia coarctata* (Forbes, 1840) at site D17 (Table 2). Eleven species were shared by sites D2 and D17, of which *C. chinensis*, *Gibbula cineraria* (Linnaeus, 1758), *G. magus* (Linnaeus, 1758) and *Chrysallida terebellum* (Philippi, 1844) were present in at least half of the monthly samples at both sites and had a numerical dominance of between 2–16%.

Temporal dynamics

The total number of species showed a marked variation through time at the three sites (Fig. 2a); numbers increased between the end of spring and the beginning of summer and then declined from September-October to February. At site D2, the number of individuals did not show any remarkable variation through most of the year the exception being in September, when *Rissoa parva* showed its greatest numerical dominance (Fig. 2b, 3b). Total abundance was low between February and June at site D17; the number of individuals increased between June and August and decreased in the following months, showing at the end of the study similar values to those found at the beginning. Site D15 showed a similar pattern to site D17

but the total abundance was in general lower than in D17. Values of diversity (H') were greater at sites D2 and D17 than at site D15, and showed great variations through the year at the three sites (Fig. 2c). The greatest values were recorded, in general, between the end of summer and the end of autumn. Evenness (J') had greater values at site D2 and D17 than at site D15 although this was not true for July and January (Fig. 2d). At site D2, the lowest values of evenness were recorded in March, July and September, otherwise those were more or less constant and about 0.8 or greater. At site D17, evenness showed a similar pattern to that of D2; the lowest values were found in February and June 1996. At site D15, values of evenness were, in general, greater between summer and the beginning of autumn than in the rest of the year. At the three sites, all univariate parameters apart from evenness at site D17 showed highly significant differences between sampling dates (Table 3); SNK tests only detected significant differences among groups of samples for number of individuals at sites D2 and D17.

At site D2, most of the numerically dominant species had their greatest abundance between August and November, and mostly from September to October. On the contrary, the opisthobranch *Cylichnina umbilicata* (Montagu, 1803) showed peaks in abundance in spring and beginning of summer. *Nassarius reticulatus* was abundant all the year round (18–118 ind. m^{-2} ; Fig. 3a); *Rissoa parva* had a peak of abundance in September of >5,000 individuals per m^2 (Fig. 3b). The only two species present in numbers at site D15 were *N. reticulatus* and *R. parva*; those species showed their greatest abundance in summer and autumn (Fig. 3c, d). At site D17, temporal patterns of abundance were similar to those of site D2; the dominant species showed peaks of abundance in summer and autumn (Fig. 3e, f). At this site, *R. parva* showed its greatest numbers in August; this species was better represented numerically at site D2 than at site D17. *Nassarius reticulatus* was present in numbers in all monthly samples; this snail was more abundant at site D17 than at the other two sites. This species showed a trend in

increasing abundance from summer to autumn but also showed great fluctuations between consecutive samplings within the same season. Other species, such as *Turritella communis*, *Gibbula cineraria*, *G. magus* and *Calyptraea chinensis*, were more abundant at site D17 than at the other two; these species showed their greatest numbers in August and October.

Multivariate analyses

For site D2, SIMPROF test recognised two different groups of monthly samples from the dendrogram based on abundance data of species: one group constituted by samples from September and October and a larger group composed by all the remaining samples (Fig. 4).

SIMPROF did not detect significant groups of samples for site D15 but the graphic representation of the nMDS showed a certain seasonality in the ordination of samples: those from summer-autumn were located on the left and those of winter-spring on the right.

Samples of site D17 were grouped into four significant clusters: two of them corresponded to samples from summer to winter and the other two from winter and spring. In general, nMDS ordinations for the three sites show that samples from the end of summer and autumn tend to be plotted together.

Gastropod fauna and sedimentary features

Analyses of correlation through the Spearman's correlation coefficient showed that, at site D15, grain-size median and coarser granulometric fractions (>0.25 mm) were negatively correlated with univariate parameters but those values were not significant ($P > 0.05$). For the other two sites, correlations did not show any clear pattern and were, in general, not significant. Similarly, the BIO-ENV procedure showed low correlations among faunistic data and any combination of sedimentary features for the three sites (site D2, $pw < 0.2$; site D15, $pw < 0.3$; site D17, $pw < 0.4$).

Discussion

The temporal evolution of gastropod fauna of the three studied sites showed seasonal trends similar to those reported from benthic assemblages inhabiting shallow subtidal sandy sediments at temperate latitudes (e.g. *western Baltic Sea*: Arntz and Rumohr 1982; *North Sea*: Van Hoey et al. 2007; *Atlantic coast of France*: Sanz 1986; *southern Iberian Peninsula*: Rueda et al. 2001; *western Mediterranean Sea*: Albertelli and Fraschetti 1995; *western North Atlantic*: Holland et al. 1987). This seasonality was mostly due to variations in the number of species of the assemblage and density of the numerically dominant species through time; maximal abundances were recorded by the end of summer and the beginning of autumn. Furthermore, correlations among faunistic data and the measured sedimentary variables were weak.

In many cases, intra-annual seasonality in faunistic attributes of the assemblage (e.g., composition, abundance, diversity) are related to patterns of recruitment and seasonal variations in food supply (Nichols and Thompson 1985; Rueda et al. 2001; Reiss and Kröncke 2005). In addition, predation and hydrodynamic stress during winter might be responsible for decrease in abundance of species (Reiss and Kröncke 2005). These facts would explain the lower values of abundance and number of species during winter and early spring in our samples; recruitment occurring during spring and an increase in food supply would lead to a posterior recovery of the assemblage. In our case, abundance and number of species were also high in early autumn as it happens in Brittany (e.g. Ibanez and Dauvin 1988); this fact has been attributed to recruitment happening not only in spring but also in summer. However, in other European areas maximal values for these parameters are usually reported for spring and summer (Sardá et al. 1995; Rueda et al. 2001; Van Hoey et al. 2007). In the Galician rias, this situation might be related to the high primary production. In fact, upwelling events are known

to occur in the rias usually twice a year, namely in spring and autumn, due to the particular hydroclimatic conditions and geographic features (Tenore et al. 1995; Figueiras et al. 2002). This grants *a priori* an important food supply until autumn which might favour to recruits from summer-autumn.

Temporal variations in abundance of some species may also be related to changes in reproductive activity and behaviour through the year. For example, some amphipods are known to migrate to deeper sediments as a reaction to changing environmental conditions (Beare and Moore 1996). In the three studied sites, the dogwhelk, *Nassarius reticulatus*, showed temporal fluctuations in numbers among seasons but also within seasons, mostly at sites D2 and D17 (cf. Fig. 3a, e). This species is common in coastal and estuarine habitats in Europe (Barroso et al. 2005) and shows complex behavioural responses to the environmental conditions (Tallmark 1980; Lambeck 1984); for instance, *N. reticulatus* is known to take advantage of high mortality of other benthic organisms by feeding on them (Van Hoey et al. 2007). During spring, *N. reticulatus* migrates inshore for mating, concentrating in particular areas and may return to deeper waters in autumn (Rasmussen 1973; Tallmark 1980); individuals of different sizes also segregate spatially to avoid intraspecific competition (Tallmark 1980). This behavioural plasticity might explain the aforementioned changes in abundance between consecutive sampling periods, which would overlap to seasonal changes in abundance due to recruitment and survival.

Univariate measures showed, in general, lower values at site D15 than at the other two sites; the former also had a poorer gastropod fauna in number of species. In addition, samples from winter and early spring at site D15 showed the lowest annual values for number of individuals and species. This could be explained in part by the greater unstability of the sediment. In fact, this site is shallower than the other studied sites, it is located close to the surf zone of the largest sandy beach in the inlet and therefore is subjected *a priori* to a greater

hydrodynamism. Sediments of the surf zone are usually environments of great hydrodynamic energy (Barros et al. 2001) which translates in frequent changes in sedimentary composition and an exacerbated physical stress for the benthic fauna. In addition, hydrodynamic events associated to winter storms also affects the infauna by removing, mobilizing or burying established populations in any given area (Dobbs and Mozarik 1983; Probert 1984; Reiss and Kröncke 2005), and resuspending potential sources of food such as carrion (Chatzinikolaou and Richardson 2008); this may also lead to the disappearance of most of the macrofauna in such conditions (Carpentier et al. 1997). In fact, the grain-size median at site D15 shifted to the medium sand fraction during February 1997 when strong storms happened in the area; on the contrary, the sediment was mostly composed by the fine and very fine sand fractions for most of the year (Moreira et al. 2008). Thus, physical stress derived from hydrodynamism and disturbance of sediment would affect negatively the gastropod assemblage. Moreover, the temporal dynamics of the assemblage of peracarid crustaceans at site D15 shows a similar pattern to that of the gastropods (Moreira et al. 2008).

Although sedimentary variables did not show significant correlations with data of temporal evolution of fauna, sediment heterogeneity may explain differences in the composition of the gastropod assemblage among sampling sites (De Grave 1999; Barros 2005). Thus, the sedimentary substratum at sites D2 and D17 is more heterogenous than that at site D15, due to the presence of scattered mats of the seagrass *Zostera marina* at D2 and of shells of large dead bivalves at both sites (e.g. *Lutraria* spp. and venerids). This greater habitat heterogeneity may allow the presence of a greater number of species at those sediments than at the more homogenous and unstable sediment found at site D15. On the one hand, the presence of bioclastic components such as mollusc shells favours the presence of epifaunal species, e.g. trochids, rissoids or the calyptraeid, *Calyptraea chinensis* (Rueda and Salas 2003), which otherwise are not present on other sediments. On the other hand,

sediments colonized by *Z. marina* are known to support a greater diversity of species than bare sediments because the seagrass increases the heterogeneity of habitat, offers protection against predators and constitutes indirectly a source of food for grazers on epiphytes and microalgae (Orth 1977; Boström and Bonsdorff 1997; Arroyo et al. 2006). Thus, the greater abundance of the rissoid snail, *Rissoa parva*, at site D2 than at the other two sites may undoubtedly be linked to the latter fact. Moreover, numbers of this species were greater at site D2 at the end of summer before the decline of the seagrass; this pattern has also been reported for several rissoids (*southern Iberian Peninsula*: Arroyo et al. 2006; Rueda and Salas 2008; Rueda et al. 2008) and other epibenthic gastropod grazers (*Japan*: Toyohara et al. 1999; Nakaoka et al. 2001).

In conclusion, temporal evolution of the gastropod assemblages at sandy sediments of the Ensenada de Baiona shows seasonal trends that are related to both biotic and abiotic features; variations in preponderance of any given factor through the year will determine the intra-annual variability of the assemblage (Reiss and Kröncke 2005). Nevertheless, the patterns found here should be contrasted in the future with long-term data series in order to investigate inter-annual variability; this variability is known to happen in temperate waters due to global events rather than local (Van Hoey et al. 2007).

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Figure legends

Fig. 1 Location of the Ensenada de Baiona and sampling sites

Fig. 2 Temporal variation in (a) number of species, (b) number of individuals, (c) Shannon-Wiener's diversity index and (d) Pielou's evenness (mean per replicate \pm standard error) at the three study sites in the Ensenada de Baiona. Black bars, site D2; white bars, site D15; grey bars, site D17

Fig. 3 Temporal variation in density (individuals per m^{-2}) of *Nassarius reticulatus* and *Rissoa parva* at sites D2 (a–b), D15 (c–d) and D17 (e–f)

Fig. 4 nMDS ordination of monthly samples (centroids calculated on abundance data) for the three sites studied. (a) site D2; (b) site D15; (c) site D17. Groups of samples determined by the SIMPROF test are shown. Sample of February 1996 for site D15 is not shown for the sake of clarity in the visualization of the ordination of the remaining samples

Table 1 Geographical coordinates and summary of abiotic and biotic characteristics of the three sampling sites

	Sampling site		
	D2	D15	D17
Latitude	42°08'50"N	42°07'50"N	42°07'30"N
Longitude	08°50'15"W	08°49'13"W	08°50'15"W
Depth (m)	7	4	7
Gravel (%)	6.56 \pm 8.05	0.27 \pm 0.58	5.41 \pm 7.94
Sand (%)	89.78 \pm 8.37	94.70 \pm 2.33	88.80 \pm 8.00
Silt/Clay (%)	3.66 \pm 1.45	5.03 \pm 2.51	5.80 \pm 1.92
Q ₅₀ (mm)	0.27 \pm 0.18	0.16 \pm 0.06	0.25 \pm 0.14
S ₀	poor to moderately well-sorted	moderate	bad to moderate
TOM (%)	1.72 \pm 0.28	2.26 \pm 0.32	3.05 \pm 0.44
N	64–5,982 (2,499)	4–254 (334)	46–2,725 (2,630)
S	6–19 (28)	1–7 (18)	6–23 (40)
H'	1.06–3.26	0–1.88	2.20–3.59

J'

0.25–0.91

0.28–0.87

0.66–0.85

Values of abiotic features expressed as mean \pm standard deviation. Q_{50} , grain-size median; S_o , sorting coefficient; N, number of individuals (range of monthly abundance expressed in individuals per m^2 ; in brackets total number of specimens collected during the whole period of study); S, number of species (range of total monthly number of species; in brackets total number of species found in the whole period of study); H' , Shannon-Wiener's diversity index (range of monthly values); J' , Pielou's evenness (range of monthly values)

Table 2 Mean monthly density (individuals per m^2), total numerical dominance (%) and presence (%) of dominant (>1%) and/or most frequent (>50%) species at any of the three sampling sites

Species	Sampling site					
	D2			D15		
	Mean abundance (\pm SD)	Dominance (%)	Presence (%)	Mean abundance (\pm SD)	Dominance (%)	Presence (%)
<i>Gibbula cineraria</i>	22.0 \pm 52.5	3.2	54	-	-	-
<i>Gibbula magus</i>	-	-	-	-	-	-
<i>Rissoa parva</i>	421.2 \pm 1,414.7	61.3	85	11.8 \pm 16.2	12.9	54
<i>Caecum trachea</i>	12.6 \pm 17.9	1.8	85	0.8 \pm 2.1	0.9	15
<i>Turritella communis</i>	-	-	-	-	-	-
<i>Calyptraea chinensis</i>	12.4 \pm 21.9	1.8	69	-	-	-
<i>Euspira pulchella</i>	4.9 \pm 4.0	0.7	77	-	-	-
<i>Nassarius pygmaeus</i>	6.9 \pm 5.9	1.0	85	0.8 \pm 2.1	0.9	15
<i>Nassarius reticulatus</i>	53.6 \pm 29.3	7.8	100	70.1 \pm 54.6	76.3	92
<i>Bela nebula</i>	9.1 \pm 7.8	1.3	77	2.7 \pm 4.9	3.0	31
<i>Mangelia coarctata</i>	1.1 \pm 4.0	0.2	8	-	-	-
<i>Chrysallida terebellum</i>	24.5 \pm 31.3	3.6	62	-	-	-
<i>Turbonilla pusilla</i>	-	-	-	0.5 \pm 1.3	0.6	15
<i>Cylichnina umbilicata</i>	36.5 \pm 45.9	5.3	77	-	-	-

<i>Retusa truncatula</i>	13.7 ± 16.6	2.0	69	0.3 ± 1.0	0.3	0.8
Total dominance (%)		90.0			94.9	

Table 3 Summary of ANOVA results for comparisons of number of species (S), number of individuals (N), Shannon-Wiener's diversity index (H') and Pielou's evenness (J') among sampling dates for each site. n = 5; df = 12; ns, not significant ($P > 0.05$); * $P < 0.01$; ** $P < 0.001$. Results of SNK tests are only shown when significant

	Sampling site		
	D2	D15	D17
S	F = 5.95 **	F = 4.34 **	F = 6.73 **
N	F = 15.15 **	F = 6.39 **	F = 5.19 **
	SNK: September > other samples (12) **		SNK: August > other samples (12) **
H'	F = 3.54 **	F = 3.90 **	F = 5.72 **
J'	F = 3.39 *	F = 4.11 **	F = 1.16 ns