REGIONAL-SCALE COMPOSITIONAL AND SIZE FIDELITY OF ROCKY INTERTIDAL COMMUNITIES FROM THE PATAGONIAN ATLANTIC COAST

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ABSTRACT: The use of rocky intertidal assemblages in paleoecology and conservation paleobiology studies is limited because these environments have low preservation potential. Here, we evaluate the fidelity between living intertidal mussel bed communities (life assemblages or LAs) and mollusk shell accumulations (death assemblages or DAs) from the environmentally harsh Patagonian Atlantic Coast. LAs were sampled from rocky mid-intertidal and mussel-dominated habitats while DAs were collected from the high water mark at beaches in close proximity to the living intertidal community to assess live-dead mismatch at regional scales. DAs were restricted to the subset of species in the DAs that inhabit rocky intertidal habitats. A total of 37,193 mollusk specimens from 15 intertidal species were included in the analysis. Ten species were present in LAs, 14 in DAs, and nine were shared by LAs and DAs. DAs showed higher diversity, less dominance, and more rare species than LAs. Despite finding good agreement in species composition between DAs and LAs within the same region, smaller species are underrepresented, as shown by differences in size-frequency distributions. Our findings indicate that the composition of DAs is a result of the combined effects of spatial and temporal averaging, size-related biases, and biases related to low detectability of boring and vagile species in LAs. Thus, DAs do not accurately detect within-provincial latitudinal gradients in composition. However, DAs clearly capture differences between the Argentine–Magellanic Transition Zone and the Magellanic Province, indicating that DAs are informative tools at regional scales despite the environmental harshness to which they are subjected.

INTRODUCTION

The degree of fidelity between living communities and their fossil counterparts constrains the usefulness of preserved assemblages to reconstruct past ecosystems. Determining how much of the biological signal reaches shell beds after the influence of biological and physical agents and time averaging, and how this preservability varies in time and space, remains one of the key steps in paleontological analysis (Fürsich 1978, 1995; Kidwell 1985, 1986, 2001; Kidwell et al. 1986; Fürsich and Aberhan 1990; Kidwell and Flessa 1995; Kowalewski et al. 2003; Tomašových et al. 2006). Previous contributions have found that there is fairly good agreement between the species composition of living assemblages (LAs) and the co-occurring death assemblages (DAs) in marine environments (e.g., Fürsich and Flessa 1987; Kidwell 2001, 2002, 2013; see examples in Kidwell and Bosence 1991) as well as in other settings and/or taxa, such as land snails (Yanes et al. 2008; Yanes 2011), fresh water mollusks (De Francesco et al. 2013; Erthal et al. 2011; Tietze and De Francesco 2012), marine mammals (Liebig et al. 2003), ungulate mammals (Miller 2011, 2012), nonvolant terrestrial mammals (Miller et al. 2014), and small mammals (Terry 2010; see other examples in Kidwell and Tomašových 2013). However, the degree of similarity between living communities and the corresponding dead remains shows a large variation (Kidwell 2001), particularly among marine benthic communities (Kidwell and Bosence 1991; Zuschin et al. 2000; Zuschin and Oliver 2003; Albano and Sabelli 2011; Feser and Miller 2014). The dissimilarities between LAs

and DAs in marine soft-bottom environments can be largely explained by the effect of time averaging and probably less by taphonomic biases (Tomašových and Kidwell 2009, 2010, 2011; Kidwell and Tomašových 2013). This finding has also been established in several other contributions both from terrestrial and marine ecosystems (Kidwell and Tomašových 2013 and references therein). A conservative estimation of the effects of time averaging on DAs indicates that in a few decades to centuries, alpha diversity increases and beta diversity decreases at small spatial scales, species dominance is reduced, and rare species become more common (i.e., rank abundance distributions become flatter) (Tomašových and Kidwell 2010).

The composition of snapshot-like LAs (i.e., sampled at a single time) is not necessarily an accurate estimate of the composition of the source assemblages from which DAs originate (i.e., integrated over a longer time). Short-term changes in species composition in living communities can be substantial (Kidwell and Bosence 1991) and compositional variations can also be enhanced by anthropogenic effects (Kidwell 2007). In addition, sampling living marine communities can be costly and logistically complicated (Warwick and Light 2002). An example of the changes that living communities experience over short time intervals that can strongly influence the results of discrete sampling (censuses) of LAs can be seen in the surf clam *Mesodesma mactroides*. This bivalve changed from being the dominant species in sandy beaches in Argentina to completely disappearing in less than a month due to a natural mass

mortality event in 1995 (Fiori and Cazzaniga 1999; Dadon 2005). The populations recovered quickly because only the benthic life stages were affected. If samples from the living communities had been taken before and after the mass mortality event, they would have been drastically different. The mass mortality of *Mytilus edulis* caused by high temperature on rocky shores represents another example (Tsuchiya 1983) (see other examples documented in Fiori and Cazzaniga 1999 and Dadon 2005). In this regard, one of the benefits of DAs is that they average out these atypical short-term events, providing a more conservative overview of community composition at broader temporal and spatial scales (Fürsich 1978; Fürsich and Aberhan 1990; Kidwell and Bosence 1991; Tomašových and Kidwell 2010; Kidwell and Tomašových 2013). The inertia of DAs to short-term changes in species composition thus turns them into good proxies for long-term or regional-scale studies of benthic assemblages.

In the southwestern Atlantic, among the most conspicuous benthic assemblages are the rocky intertidal communities. These habitats invariably consist of dense and extended monocultures of small *Brachidontes* mussels, which are very important ecosystem engineers (Olivier et al. 1966a, 1966b; Bertness et al. 2006; Adami et al. 2008, 2013). Other larger mytilids (e.g., *Mytilus* spp., *Aulacomya atra*) are also present along the rocky shores, but at low population densities (López Gappa et al. 1990; Adami et al. 2004). Intertidal mussels frequently occur as multilayered beds (Guiñez and Castilla 1999) of considerable structural complexity (Commito and Rusignuolo 2000). These mussel beds buffer other species against biotic and abiotic fluctuations, and produce an array of microhabitats that facilitates persistence of associated organisms (Silliman et al. 2011). Studies conducted in Patagonia have shown that extreme desiccation is an important and unique feature of these intertidal mussel-dominated beds (Bertness et al. 2006). Strong dry winds, combined with low rainfall probably make these shores one of the most physically demanding rocky intertidal systems in the world. These mussel beds offer an exceptional opportunity to assess the preservability of rocky intertidal communities by quantifying fidelity between LAs and DAs. In addition, most live-dead studies in marine environments have focused on soft- or mixed-sediment habitats (but see Zuschin et al. 2000; Zuschin and Oliver 2003; Zuschin and Stachowitsch 2007), while compositional fidelity in rocky-bottom intertidal environments remains poorly known.

Here, we evaluate the correspondence between mollusk DAs from Patagonian beaches that represent natural sediment traps for inhabitants of rocky intertidal communities (Martinelli et al. 2013, and additional data gathered for this study), and a database of intertidal mussel bed communities from the same area (Adami et al. 2013). We seek to establish the degree of fidelity with which compositional and ecological information from living communities is represented by DAs in this climatically harsh environment. To do this, we (1) compare LAs and DAs within two biogeographic provinces and (2) assess the regional variability of fidelity in species composition across the boundary between two biogeographic provinces (i.e., Argentine and Magellanic). Rocky shores are dominated by erosion and do not tend to accumulate any sediment, consequently dead shells are destroyed or quickly transported away to other habitats. Therefore, the nature of live-dead comparison is based on LAs and DAs sampled at different sites within the same regions, allowing regional-scale inferences on the preservability of ecological signals within and between biogeographic provinces. We hypothesize that DAs maintain the species composition from the communities from which they derive, even after suffering the biases brought about by various taphonomic agents, and the effects of time averaging. In particular, we predict that the DAs will share roughly the same species composition and abundance with the LAs. In agreement with previous studies, we also anticipate that DAs will be enriched in larger specimens (Fürsich and Oschmann 1993; Valentine et al. 2006), and will show higher taxonomic

FIG. 1.—Map of the study area with the sampled localities. Triangles represent living assemblages (LA) and circles represent death assemblages (DA). For more details see Table 1.

richness and evenness than LAs (Fürsich and Aberhan 1990; Olszewski and Kidwell 2007; Kidwell and Tomašových 2013).

MATERIALS AND METHODS

The Study System

The study region encompasses 1,500 km along the south Argentine Atlantic coastline (41–48°S; Fig. 1), including the Transition Zone between the Argentine and Magellanic Biogeographic Provinces (41°S and 43°S; Balech and Ehrlich 2008) and the northern part of the Magellanic Province (43–48°S). Both LAs and DAs from this area are exposed to high-energy flows during high tides (mean tidal amplitude ranges from 1.76 to 6.74 m, while maximum tidal amplitude varies between 2.46 and 9.57 m (Balech and Ehrlich 2008; Servicio de Hidrografía Naval 2012). Temperatures are usually low (min SST ranges between 4.2 and 10.8°C, max SST ranges between 12.9 and 20.1°C; Table 1) and winds are frequent and strong (45–140 km/h; Camacho 1979; Bertness et al. 2006).

The configuration of the Argentinean Patagonian coastal margin is the result of several factors mainly related to sea-level variations associated with glacioeustatic climate changes as well as geotectonic and isostatic compensation processes (Clapperton 1993; Rostami et al. 2000; Schellmann and Radtke 2000, 2010; Pedoja et al. 2011). The geographic distribution and the characteristics of rocky shores of our study area are listed in Table 1.

Mussel Beds in Rocky Intertidal Shores.—Several mytilid species are found in intertidal mussel beds along southwestern Atlantic coasts (Scarabino et al. 2006; Ríos 2009; Adami et al. 2013; Trovant et al. 2013). The study area is dominated by two small-sized *Brachidontes* species that form dense beds along with other species in minor proportions (i.e., *Mytilus* spp.) (Olivier et al. 1966a, 1966b; López Gappa et al. 1990; Adami et al. 2004, 2008; Bertness et al. 2006). *Brachidontes rodriguezii* dominates the rocky intertidal from Buenos Aires to northern Patagonia

TABLE 1.—*Details of the localities included in this study.*

Name and number of localities	Abbreviations	Southern latitude	Sampling date	Sample type	Substrate characteristics	Biogeographic region	Sea water temperature (°C)
Las Grutas (1)	LG_L	40° 50' 02"	Jan. 2004, 2008	Live	Friable epiclastic sediments, marine deposits (Tertiary)	Arg-Mag. Provinces transition zone	10.8–20.1
Punta Mejillón (2)	PM_L	41° 00' 51"	Jan. 2004, 2008	Live	Friable epiclastic sediments, marine deposits (Tertiary)	Arg-Mag. Provinces transition zone	10.1–18.9
Playas Doradas (3)	PD_L	41° 36' 41"	Jan. 2004, 2008	Live	Limestone, calcareous sandstone and coquina (Paleocene)	Arg-Mag. Provinces transition zone	10.1–18.9
Playas Doradas (4)	PD_D	41° 36' 41"	April 2010	Dead	Limestone, calcareous sandstone and coquina	Arg-Mag. Provinces transition zone	10.1–18.9
Puerto Lobos (5)	PL_D	41° 59' 54"	April 2010	Dead	Hard substrates of conglomerate and tuff. Sectors with fine sand beaches.	Arg-Mag. Provinces transition zone	9.7–17.9
Puerto Pirámides (6)	PP_D	42° 34' 43"	April 2010	Dead	Bottoms with sand and mud, some hard substrates. Sandy beaches. Cliffs.	Arg-Mag. Provinces transition zone	9.6–16.9
El Doradillo (7)	ED_D	42° 39' 27"	April 2010	Dead	Bottoms with sand and mud, some hard substrates. Sandy beaches.	Arg-Mag. Provinces transition zone	9.7–16.9
Puerto Madryn (8)	PM_D	42° 46' 56"	April 2010	Dead	Bottoms with sand and mud, some hard substrates. Sandy beaches.	Arg-Mag. Provinces transition zone	9.8–16.9
Punta Ninfas (9)	PN_L	42° 58' 02"	Jan. 2004, 2006	Live	Limestone. Marine deposits.	Arg-Mag. Provinces transition zone	9.4–16.8
Playa Elola (10)	PE_D	44° 50' 17"	April 2010	Dead	Beaches with sandy gravel, hard substrates with basalt; some sandy and muddy.	Magellanic Province	6.4–16.1
Camarones (11)	CA_L	44° 54' 34"	Jan. 2004	Live	Consolidated limestone. Shores of basaltic rock.	Magellanic Province	7.3–16.2
Rada Tilly (12) Caleta Olivia (13)	RT_D	45° 56' 37"	April 2010	Dead	Limestone. Marine deposits.	Magellanic Province	6.5–15.5
	CO_L	46° 20' 06"	Jan 2004	Live	Limestone. Marine deposits.	Magellanic Province	5.2–14
Caleta Olivia (14)	CO_D	46° 29' 29"	April 2010	Dead	Beaches with coarse sand and pebbles. Some rockgrounds in the mid-littoral area.	Magellanic Province	5.2–14
Cabo Blanco (15)	CB_D	47° 12' 09"	April 2010	Dead	Beaches with gravel and pebbles. Areas with hardgrounds with tidal forests of macroalgae.	Magellanic Province	4.2–12.9
Puerto Deseado (16)	PuD_D	47° 45' 24"	April 2010	Dead	Gravel beaches, some cliffs with sandy beaches, and sectors with hardgrounds.	Magellanic Province	4.9–13.5

(Penchaszadeh 1973; López Gappa et al. 1990; Adami et al. 2004; Adami et al. 2013), and *Brachidontes* (= *Perumytilus*) *purpuratus* is most abundant from northern Patagonia to the Pacific Ocean coast up to Ecuador (Bernard 1983). Both species coexist in the Transition Zone between the Argentine and Magellanic Biogeographic provinces (41–43°S) and, although both species are morphologically and biologically very similar, the structure of their mussel beds and their accompanying fauna differ significantly (Arribas et al. 2013).

Methods

Two databases were used for the live-dead comparisons. The first one has exhaustive counts of living mollusks (LAs) from the middle rocky intertidal from six localities along the Atlantic coast of Patagonia (Fig. 1, Table 1). The second database contains counts of intertidal mollusks from death assemblages sampled at ten localities within same region (Fig. 1, Table 1). Because rocky-bottom habitats are dominated by erosional processes, and hence do not accumulate shells, DAs were collected at beaches where shells from intertidal and subtidal habitats accumulated, and locations of LAs thus do not precisely coincide with locations of DAs. The selection of sites where DAs were sampled was designed to capture the spatial variation in species composition of shell accumulations in the study area. However, out of 16 localities, three localities with DAs are located close to localities with LAs (localities 3 and 4 at Playas Doradas, localities 10 and 11 at Playa Elola/Camarones,

and localities 13 and 14 at Caleta Olivia), thus forming three pairs of LAs and DAs that can be compared at smaller spatial scales (see Table 1 for latitude details). To make the samples of DAs comparable with those from LAs, we selected the subset of species that occur in rocky intertidal habitats on the basis of evidence independent from LA composition (i.e., from published literature and/or field observation of some of the authors, namely FA, SG, MA and JM, during different field seasons) (Table 2).

Sampling.—Living assemblages (LAs) were sampled at six localities between 2004 and 2008 (Table 1) (Adami et al. 2013). In every locality five or six replicates of 14×14 cm (200 cm^2) were taken and all living specimens counted. The replicates were randomly spread at each sampling site. Samples were always obtained from the mid-intertidal zone, aiming at the centroid of patches with 100% mussel cover developed over gently sloping surfaces (Fig. 2A, B). Samples were sieved using a 0.5 mm mesh, and mussels and other macrofaunal organisms were retrieved.

Death assemblages (DAs) were collected in April 2010 at ten localities along the Atlantic coast of Patagonia (Table 1). The high-water mark was sampled every 10 m using a 0.5 m $\times$ 0.5 m quadrat (Fig. 2C, D). Shells were carefully hand collected (not sieved) from the sediment surface and in some cases as deep as 10 cm if the beach was pebbly. Depending on density, shells from 10 to 20 quadrats were combined to obtain at least 200 complete shells. Bivalve individuals were estimated as articulated shells plus the most abundant of left or right valves.

TABLE 2.—*Summary of species found in the death assemblages. Zonation (subtidal, intertidal), substrate type (H: hard, S: soft), life habit (Ep: epifaunal, In: infaunal) and species documented for intertidal rocky-bottom substrates (DRI*).*

Family	Species	Zonation	Substrate	Life habit	DRI*	Source
Gastropoda						
Nacellidae	*Nacella (P.) magellanica* (Gmelin)	Intertidal-subtidal	H	Ep	*	Charo et al. 2014
Nacellidae	*Nacella (N.) mytilina* (Helbling)	Subtidal	H	Ep		Rosenberg 2009
Fissurellidae	*Fissurella* spp.	Intertidal-subtidal	H	Ep	*	Rechimont et al. 2013
Trochidae	*Tegula (A.) patagonica* d'Orbigny	Intertidal-subtidal	H	Ep	*	Rechimont et al. 2013
Calyptraeidae	*Crepidula aculeata* (Gmelin)	Intertidal-subtidal	H	Ep	*	Scarabino et al. 2006
Calyptraeidae	*Crepidula dilatata* Lamarck	Intertidal-subtidal	H	Ep	*	Charo et al. 2014
Naticidae	*Notocochlis isabelleana* (d'Orbigny)	Intertidal-subtidal	S	In		Pastorino 1994
Epitoniidae	*Epitonium georgettina* (Kiener)	Intertidal-subtidal	S	Ep		Rosenberg 2009, Scarabino et al. 2006
Muricidae	*Trophon geversianus* (Pallas)	Intertidal-subtidal	H-S	Ep	*	Rechimont et al. 2013, Aldea and Troncoso 2010
Buccinidae	*Buccinanops globulosum* (Kiener)	Intertidal-subtidal	S	Ep		Charo et al. 2014, Gonzalez et al. 2011, Scarabino et al. 2006
Buccinidae	*Buccinanops* sp.	Intertidal-subtidal	S	Ep		Charo et al. 2014, Gonzalez et al. 2011, Scarabino et al. 2006
Buccinulidae	*Pareuthria plumbea* (Philippi)	Intertidal-subtidal	H	Ep	*	Wieters et al. 2012
Olividae	*Olivancillaria carcellesi* Klappenbach	Intertidal-subtidal	S	Ep		Charo et al. 2013, Scarabino et al. 2006, Teso et al. 2011
Olivellidae	*Olivella tehuelcha* (Duclos)	Subtidal	S	Ep		Charo et al. 2014
Volutidae	*Odontocymbiola magellanica* (Gmelin)	Subtidal	S	Ep		Bigatti et al. 2008
Siphonariidae	*Siphonaria lessonii* (Blainville)	Intertidal	H	Ep	*	Adami 2008, Bertness et al. 2006, Wieters et al. 2012
Bivalvia						
Pectinidae	*Aequipecten tehuelchus* (d'Orbigny)	Subtidal	H	Ep		Charo et al. 2014
Mytilidae	*Lithophaga patagonica* (d'Orbigny)	Intertidal-subtidal	H	Ep	*	Rechimont et al. 2013
Mytilidae	*Aulacomya atra* (Molina)	Intertidal-subtidal	H	Ep	*	Charo et al. 2014, Rechimont et al. 2013
Mytilidae	*Brachidontes purpuratus* (Lamarck)	Intertidal-subtidal	H	Ep	*	Adami et al. 2013, Rechimont et al. 2013
Mytilidae	*Brachidontes rodriguezii* d'Orbigny	Intertidal-subtidal	H	Ep	*	Adami et al. 2013, Rechimont et al. 2013
Mytilidae	*Mytilus edulis chilensis* Hupé	Intertidal-subtidal	H	Ep	*	Cuevas et al. 2006, Rosenberg 2009
Mytilidae	*Mytilus edulis platensis* d'Orbigny	Intertidal-subtidal	H	Ep	*	Adami et al. 2004, Charo et al. 2014
Solenidae	*Ensis macha* (Molina)	Intertidal-subtidal	S	In		Márquez and Van der Molen 2011
Mactridae	*Mactra isabelleana* d'Orbigny	Subtidal	S	In		Signorelli and Pastorino 2011, Signorelli et al. 2013
Tellinidae	*Macoma* sp.	Subtidal	S	In		Charo et al. 2013
Tellinidae	*Tellina petitiana* d'Orbigny	Subtidal	S	In		Pastorino 1994, Rosenberg 2009
Veneridae	*Amiantis purpurata* (Lamarck)	Intertidal-subtidal	S	In		Morsan 2007
Veneridae	*Retrotapes exalbidus* (Dillwyn)	Subtidal	S	In		Charo et al. 2014, Lomovasky et al. 2002
Veneridae	*Tawera gayi* (Hupé)	Subtidal	S	In		Gordillo 2006, Lomovasky et al. 2005
Veneridae	*Ameghinomya antiqua* King and Broderip	Subtidal	S	In		Rosenberg 2009
Petricolidae	*Petricola (P.) pholadiformis* Lamarck	Intertidal-subtidal	S	In		Rosenberg 2009
Semelidae	*Semele proficua* (Pulteney)	Intertidal-subtidal	S	In		Pastorino 1994, Rosenberg 2009
Hiatellidae	*Panopea abbreviata* Valenciennes	Subtidal	S	In		Rosenberg 2009

Univariate and Multivariate Analyses.—Species richness (S) and the PIE index (probability of interspecific encounter) were calculated for all LAs and DAs using PAST (Hammer et al. 2001). PIE is an evenness index related to Simpson's index of diversity (Hulbert 1971; Hammer and Harper 2006). Owing to the different sample sizes we also estimated species richness with rarefaction for $n = 301$ with PAST (Hammer et al. 2001). Differences in abundance of the most common species between LAs and DAs were graphically compared with bar plots. These plots were constructed for Playas Doradas (localities 3 and 4), Playa Elola/ Camarones (localities 10 and 11), and Caleta Olivia (localities 13 and 14). Similar graphical representations were used to compare LAs and DAs at the provincial level. For analyses at the provincial scale we calculated the average percentage of each species across all localities in the corresponding biogeographic unit and type of sample (DA or LA).

A nonmetric multidimensional scaling (NMDS) was used to assess the similarity in species composition among LAs and DAs. A matrix was built with all the mollusk species from both databases (15 species; $n = 37,193$ individuals). Absolute abundances were standardized to percentages, and then transformed with (a) square root and (b) presence–absence. The Bray-Curtis distance was used for abundance data (Clarke 1993; Clarke and Warwick 2001; Clarke et al. 2006) and Sorensen coefficient for binary data (Hammer et al. 2001) (The Sorensen coefficient is equivalent to the Bray-Curtis distance applied to presence/absence data). Plots were rotated in order to arrange samples latitudinally. NMDS was performed with R (R Core Team 2014). Differences in species composition on the basis of percentages between LAs and DAs were assessed with a one-way PERMANOVA test (nonparametric multivariate analysis of variance) using Bray-Curtis as a distance index, using PAST (Hammer et al. 2001). This analysis was done for the whole matrix and by biogeographic province, with 9,999 permutations. The same procedure was used to compare species composition between biogeographic provinces for DAs and LAs.

In order to test the hypothesis that size-selective biostratinomic factors (tides, waves, and wind) affect the preservation of shells in DAs, we compared the size-frequency distributions of living and dead specimens of *B. purpuratus* and *B. rodriguezii*. We predicted that physical agents

FIG. 2.—**A**) View of a mussel bed in Bahía Camarones (CA-L). **B**) Detail of a mussel bed. **C**) View of high tide line accumulation of dead shells. **D**) Sampling of death assemblages. The size of the quadrat is 50 × 50 cm.

TABLE 3.— *Information of samples of living and death assemblages used in the analysis.*

Sample number	Locality	Abbreviation	Sample type	N (individuals number)	Species richness (S)	Rarefaction S (n=301)	PIE evenness
1	Las Grutas	LG_L	Live	3903	4	2.80	0.10
2	Punta Mejillón	PM_L	Live	5573	6	5.00	0.30
3	Playas Doradas	PD_L	Live	3564	6	4.27	0.46
4	Playas Doradas	PD_D	Dead	634	11	10.65	0.57
5	Puerto Lobos	PL_D	Dead	1778	11	10.11	0.72
6	Puerto Pirámides	PP_D	Dead	1094	11	8.86	0.67
7	El Doradillo	ED_D	Dead	913	10	9.32	0.78
8	Puerto Madryn	PM_D	Dead	3013	11	8.41	0.58
9	Punta Ninfas	PN_L	Live	2772	7	3.88	0.26
10	Playa Elola	PE_D	Dead	401	8	8.00	0.71
11	Camarones	CA_L	Live	6255	4	2.89	0.35
12	Rada Tilly	RT_D	Dead	341	8	7.87	0.53
13	Caleta Olivia	CO_L	Live	5329	7	3.08	0.05
14	Caleta Olivia	CO_D	Dead	602	7	6.86	0.71
15	Cabo Blanco	CB_D	Dead	295	8	8.00	0.56
16	Puerto Deseado	PuD_D	Dead	726	6	5.84	0.63

Intertidal vs. subtidal | Hard vs. soft substrate (only intertidal)

A - Abundance

Subtidal 390 specimens

Intertidal: 10,949 specimens

Intertidal, soft substrates: 1,152 specimens

Intertidal, rocky substrates: 9,797 specimens

B - Species richness

Subtidal: 10 species

Intertidal: 24 species

Intertidal, rocky substrates: 14 species
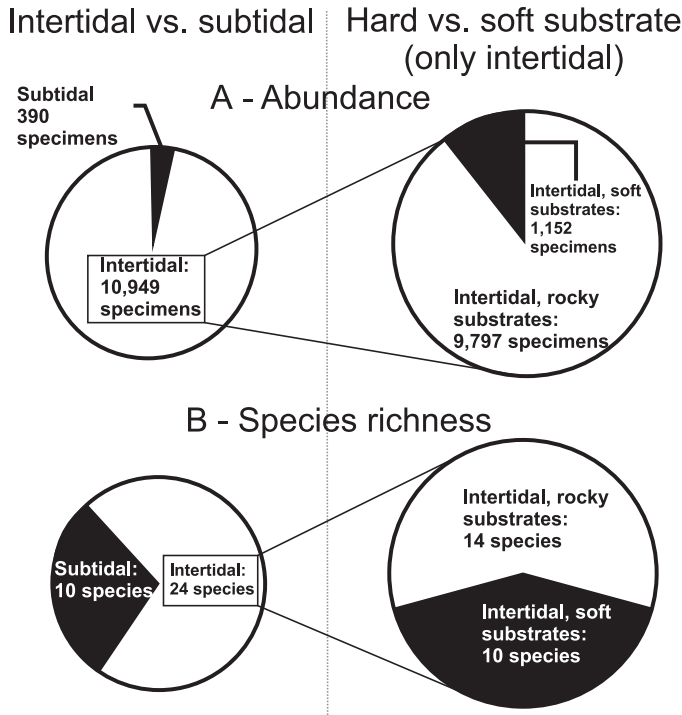
Intertidal, soft substrates: 10 species

Fig. 3.—Pie charts with details of the distribution of abundance and species richness of death assemblages for data pooled across samples. **A)** Absolute abundance. **B)** Species richness. Plots on the left side of the figure differentiate between intertidal and subtidal species while those on the right side indicate distribution of species and specimens between hard and soft substrates of the intertidal belt.

eliminate small specimens from the DAs increasing the average specimen size and/or causing the displacement of size-frequency distribution (SFDs) of DAs to larger sizes. For *B. rodriguezii*, we compared the size-frequency distribution for Playas Doradas (LA vs. DA), and El Doradillo (DA) vs. Punta Ninfas (LA). For *B. purpuratus* we compared the size-frequency distribution for El Doradillo (DA) vs. Punta Ninfas

(LA), Playa Elola (DA) vs. Camarones (LA), and Caleta Olivia (LA vs. DA). We measured the maximum linear dimension of the shell (length) in mm to construct size-frequency distributions. Digital calipers were used for larger mussels, and a microscope micrometer for the smaller ones. A Kolmogorov-Smirnov test was performed to detect overall differences in the distribution of the two samples. Analyses were run with PAST (Hammer et al. 2001).

RESULTS

Composition of Death Assemblages

Death assemblages consist of a mix of intertidal and subtidal species inhabiting soft and hard substrates, caused by the mosaic distribution of rocky, muddy, and sandy substrates along the sampling area. Out of the 11,339 specimens from 34 species sampled in the DAs, 86.4% (9,797 specimens, 14 species) inhabit the rocky intertidal belt and were included in the analysis (Fig. 3A, B). From the remaining 13.6%, 3.4% (360 individuals, 10 species) belong to subtidal mollusks and 10.2% correspond to soft-bottom intertidal species (1,152 specimens, 10 species). Therefore, intertidal species accounted for 96.6% of the specimens in DAs.

Compositional Fidelity

A total of 37,193 specimens from 15 species were included in the analysis (LA: 27,396; DA: 9,797, Table 3). Of the 15 species, ten were found in the LAs, 14 in DAs, and nine species in both assemblage types. One species found in the LAs was absent in samples from dead shell accumulations (*Lasaea* sp., see below, Table 4). Conversely, five species detected in DAs were not found in living communities. These dead-only species were one lithophagid mytilid (*Lithophaga patagonica*), two Calyptraeidae (*Crepidula aculeata* and *C. dilatata*), the limpet *Nacella magellanica*, and the snail *Tegula patagonica* (Table 4). Large mytilids (*Aulacomya atra, Mytilus edulis chilensis*, and *M. edulis platensis*) are scarce in living middle intertidal communities, but present or even abundant in DAs (Table 4).

Diversity was consistently higher in DAs than in LAs (Table 3). Species richness was highly variable in the DAs, and consistently low in the LAs (Fig. 4A). PIE evenness index was higher in DAs (Fig. 4B). Rarefaction of species richness to $n = 301$ individuals confirms the higher species richness in DAs (Fig. 4C).

TABLE 4.—*Species counts per sample.*

Species	LG_L	PM_L	PD_L	PD_D	PL_D	PP_D	ED_D	PM_D	PN_L	PE_D	CA_L	RT_D	CO_L	CO_D	CB_D	PuD_D
Aulacomya atra (Molina)	0	0	0	18	68	3	215	38	0	65	1	23	1	142	9	110
Brachidontes purpuratus (Lamarck)	196	373	2436	2	885	543	103	438	2358	192	4873	38	5187	227	68	384
Brachidontes rodriguezii d'Orbigny	3694	4617	982	69	179	231	25	244	314	0	0	0	0	0	0	0
Crepidula aculeata (Gmelin)	0	0	0	4	1	0	0	1	0	0	0	0	0	0	0	0
Crepidula dilatata Lamarck	0	0	0	17	15	1	41	71	0	12	0	28	0	8	13	0
Fissurella sp.	0	0	0	26	50	5	13	1	1	0	0	0	0	0	1	0
Lithophaga patagonica (d'Orbigny)	0	0	0	0	0	1	1	3	0	0	0	0	0	0	0	0
Mytilus edulis chilensis Hupé	0	0	0	0	0	7	0	0	1	5	0	229	1	7	184	184
Mytilus edulis platensis d'Orbigny	5	106	4	10	93	25	17	30	0	0	0	0	0	0	0	0
Nacella (P.) magellanica (Gmelin)	0	0	0	11	67	0	0	0	0	48	0	9	0	182	10	38
Pareuthria plumbea (Philippi)	0	0	0	0	0	0	0	0	0	8	0	0	1	3	3	6
Siphonaria lessonii (Blainville)	8	52	116	21	145	191	174	180	1	53	37	2	112	0	0	0
Tegula patagonica d'Orbigny	0	0	0	406	129	69	307	1885	0	0	0	1	0	0	0	0
Trophon geversianus (Pallas)	0	1	1	50	146	18	17	122	7	18	0	11	3	33	7	4
Lasaea sp.	0	424	25	0	0	0	0	0	90	0	1344	0	24	0	0	0

A - Species richness (S)

B - Hulbert's PIE

C - Rarefaction (n=301)

LA   DA
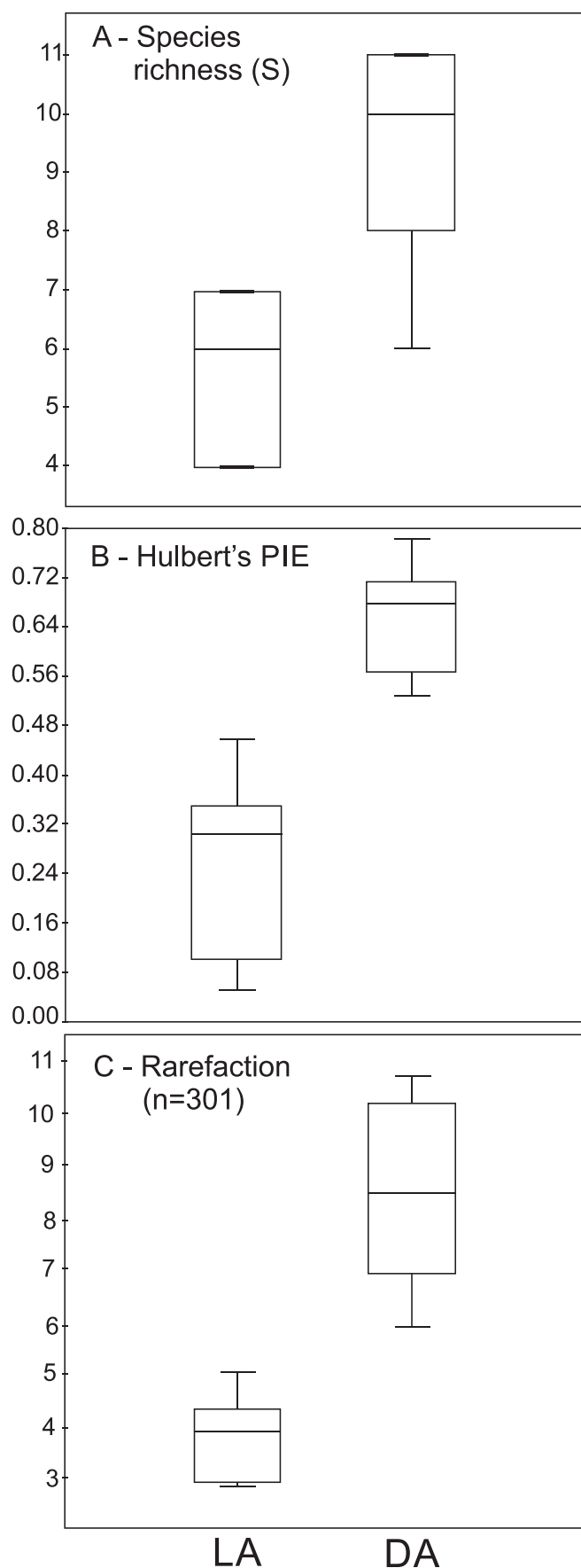
The NMDS showed that both latitude (which correlates with biogeographic affinity of localities) and assemblage type (LA versus DA) discriminate assemblages in a multivariate space (Fig. 5A, B). DAs belonging to the Argentine-Magellanic Transition Zone (localities 4 to 8) cluster together, and are separated from southern Magellanic localities (localities 10, 12, and 14–16). Living communities show a latitudinal arrangement along the y-axis of the NMDS plot (with equatorward localities on the top; Fig. 5A, B). Although DAs do not show the latitudinal signature within the two biogeographical provinces, they still clearly segregate the Transition Zone and Magellanic Province. PER-MANOVA tests confirm this observation: DAs from the Transition Zone differ significantly from those sampled in the Magellanic Province (F = 5.47; p = 0.009). The composition of LAs did not significantly differ between the Transition Zone and the Magellanic Province (F = 2.75; p = 0.133). However, this result could be an artifact of a small number of samples, with only two LAs in the Magellanic Province.

Species composition and abundance were significantly different between LAs and DAs for the full matrix (F = 4.38; p = 0.002) and for the samples from the Transition Zone between provinces (F = 4.50; p = 0.013). Within the Magellanic Province, species composition was not significantly different (F = 4.20; p = 0.096), although this result could be related to the small number of LAs in the Magellanic Province (n = 2). Comparison of species abundance between LAs and DAs from closely spaced localities at Playas Doradas (within the Transition Zone) show overrepresentation of *Tegula patagonica* and underrepresentation of *Lasaea* sp. in DAs (Fig. 6). In the cases of Camarones/Playa Elola and Caleta Olivia (in the Magellanic Province), *Aulacomya atra* and *Nacella magellanica* are overrepresented and in both cases *Lasaea* sp. is underrepresented in DAs (Fig. 6). In turn, comparisons within provinces show that *Tegula patagonica* is highly overrepresented in DAs in the Transition Zone while *Lasaea* sp. is underrepresented (Fig. 7). Within the Magellanic Province, *Mytilus edulis chilensis*, *Aulacomya atra*, and *Nacella magellanica* are overrepresented while *Lasaea* sp. is underrepresented in DAs (Fig. 7).

Size Fidelity

Dead shells of *B. purpuratus* and *B. rodriguezii* are larger than shells from living communities (p < 0.0001 in all five comparisons; Fig. 8A–E, Table 5). Size-frequency distributions of living mussels show a bimodal or multimodal distribution (frequently with high abundance of specimens smaller than 5 mm), while dead shells show a unimodal distribution with modes at ~15–20 mm (Fig. 8A–E). In addition, measurements from DAs have consistently lower variation than those taken from living communities (Table 5).

DISCUSSION

The results of our analyses show a general agreement with previous studies restricted to single habitats, mainly performed in subtidal and soft-bottom environments: 90% of the living species are found dead in the same study area, and 64% of the dead species are found alive in the same area. Summarizing these live-dead indices from various marine environments, Kidwell and Bosence (1991) showed that the live species represented in DAs range from 83% (intertidal) to 95% (coastal subtidal), while dead species found in living communities range from 33% (coastal subtidal) to 54% (intertidal).

←

Fig. 4.—Boxplots show that diversity indices are higher in DAs than LAs. **A**) Species richness (S). **B**) Evenness index (PIE). **C**) Species richness estimated by rarefaction. Boxes range from first to third quartile. Whiskers represent minimum and maximum values. LA: life assemblages. DA: death assemblages.
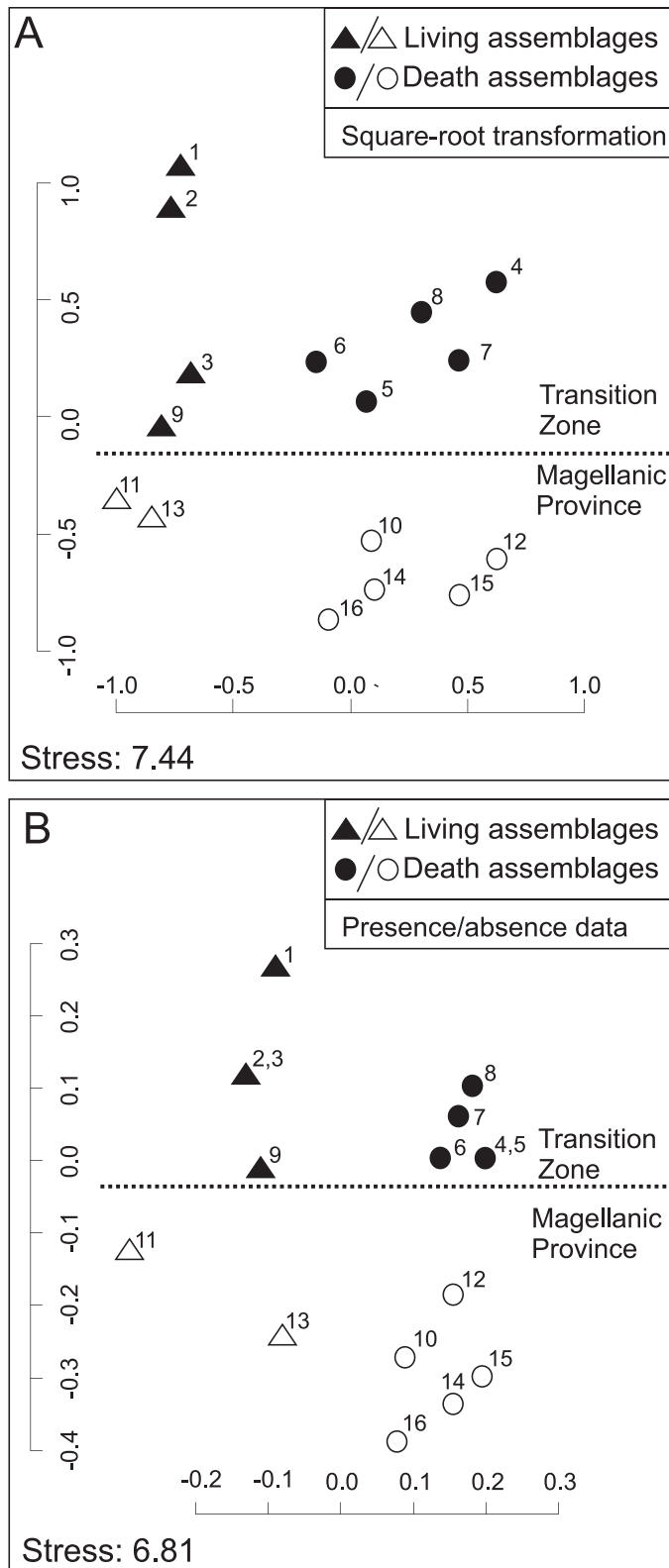
FIG. 5.—Two-dimensional NMDS plots show segregation between two provinces for both living and death assemblages but also a consistent segregation between living and death assemblages. **A**) Square-root transformation after standardization to percentages. **B**) Presence-absence data. Axes were rotated to place samples in a latitudinal order. Symbols: triangles = living assemblages; circles = death assemblages; filled symbols = Argentine-Magellanic Transition Zone; empty symbols = Magellanic Biogeographic Province.

One of the factors affecting the magnitude of live-dead agreements observed in this study could be the variability in the proportion of soft and hard substrates among localities and in the detectability of some species in LAs due to their vagile life habits. For instance, Puerto Madryn is dominated by sandy and muddy soft substrates (Table 1), which correlates with the high abundance of *Tegula patagonica* in DAs (which is absent in LAs). Similarly, the muricid *Trophon geversianus* is normally found in the lower intertidal to subtidal, and in our study it is more abundant in DAs than in LAs. Both species are vagile and are thus able to escape subaerial exposure or hide during low tides, decreasing their probability of being sampled in the LAs. Another species with particular life habits is *Lithophaga patagonica*, a bioeroder that inhabits bottle-shaped rock borings. This species is present in DAs but absent in living communities, most likely due to the low detectability caused by its cryptic life habit. A similar factor also affects the low detectability of cryptic species in LAs in hard-bottom habitats in coral reefs reported by Zuschin et al. (2000) and in offshore reefs dominated by coralline algae and *Posidonia oceanica* reported by Albano and Sabelli (2011). Also, DAs were not sieved and this fact could have added an artificial bias against small specimens, even when sampling design was developed to reduce the drawback. Finally, the possible effect of human impact on communities (Kidwell 2013) was not considered. These factors should be assessed in future studies.

Origin of Intertidal Death Assemblages

Death assemblages accumulated above the intertidal belt in Patagonian rocky shores include a mix of shallow subtidal to upper intertidal species that inhabit both hard and soft substrates. However, most specimens belong to species living in the intertidal belt (96.6%), and more than four fifths of them are hard-substrate dwellers (86.4%) (Fig. 3). These proportions suggest that the supratidal high-water mark is a good area to obtain samples from intertidal species on Patagonian shores; at the same time, our results indicate that the bathymetric mixing of faunas from intertidal and subtidal settings is minor, affecting only 3.4% of the specimens.

The formation of intertidal DAs can be explained as strandings caused by storms and high tides that move shells and live specimens from sublittoral bottoms to the swash zone and above (López et al. 2008). In our case, both storms and high tides can explain the genesis of DAs. We also observed *Mytilus* shells rolling on the beach due to strong winds, suggesting that winds can also aggregate shells into DAs.

Size-Associated Taphonomic Biases

Despite the general agreement between LAs and DAs, multivariate analyses show that DAs and LAs are compositionally segregated at all latitudes. Species that are underrepresented in DAs tend to be smaller. The absence of *Lasaea* sp. in DAs is one of the most striking examples. *Lasaea* sp. represents 7% of the abundance of the pooled samples from living communities, reaching as much as 21.5% in Puerto Madryn (Table 4). However, this species is completely absent from all DAs (Table 4). It is likely that individuals from this species could have been destroyed or transported away because they are 3 mm long and very thin and live attached to mussels by byssi (Forcelli 2000, and observations of the authors). Transportation by water is possible because minute valves are washed away during high tides, kept in suspension, and finally deposited on deeper, calmer bottoms (Fürsich 1990; Valentine et al. 2006; and observations of the authors). The strong winds in Patagonia are also able to remove these shells, and cause the small-sized mussels (< 5 mm) to be transported by the wind. This interference is consistent with the observation that body size is one of the main factors explaining the absence of living species in the fossil record (Valentine et al. 2006).

All size-frequency comparisons for *Brachidontes* species show that DAs are enriched in shells larger than 7 mm with respect to LAs (Fig. 8A–E),

Living assemblages

Percentages

Playas Doradas

	0 10 20 30 40 50 60
B. purpuratus	
B. rodriguezii	
Siphonaria lessonii	
Lasaea sp.	
M. e. platensis	
Trophon geversianus	
Tegula patagonica	
Nacella magellanica	
Fissurella sp.	
Crepidula dilatata	
Crepidula aculeata	
Aulacomya atra	

Death assemblages

Percentages

60 50 40 30 20 10 0

Tegula patagonica
B. rodriguezii
Trophon geversianus
Fissurella sp.
Siphonaria lessonii
Aulacomya atra
Crepidula dilatata
Nacella magellanica
M. e. platensis
Crepidula aculeata
B. purpuratus
Lasaea sp.

Camarones

0 10 20 30 40 50 60 70 80

B. purpuratus
Lasaea sp.
Siphonaria lessonii
Aulacomya atra
Nacella magellanica
Trophon geversianus
Crepidula dilatata
Pareuthria plumbea
M. e. chilensis

Playa Elola

60 50 40 30 20 10 0

B. purpuratus
Aulacomya atra
Siphonaria lessonii
Nacella magellanica
Trophon geversianus
Crepidula dilatata
Pareuthria plumbea
M. e. chilensis
Lasaea sp.

Caleta Olivia

0 10 20 30 40 50 60 70 80 90

B. purpuratus
Siphonaria lessonii
Lasaea sp.
Trophon geversianus
Pareuthria plumbea
M. e. chilensis
Aulacomya atra
Nacella magellanica
Crepidula dilatata

50 40 30 20 10 0

B. purpuratus
Nacella magellanica
Aulacomya atra
Trophon geversianus
Crepidula dilatata
M. e. chilensis
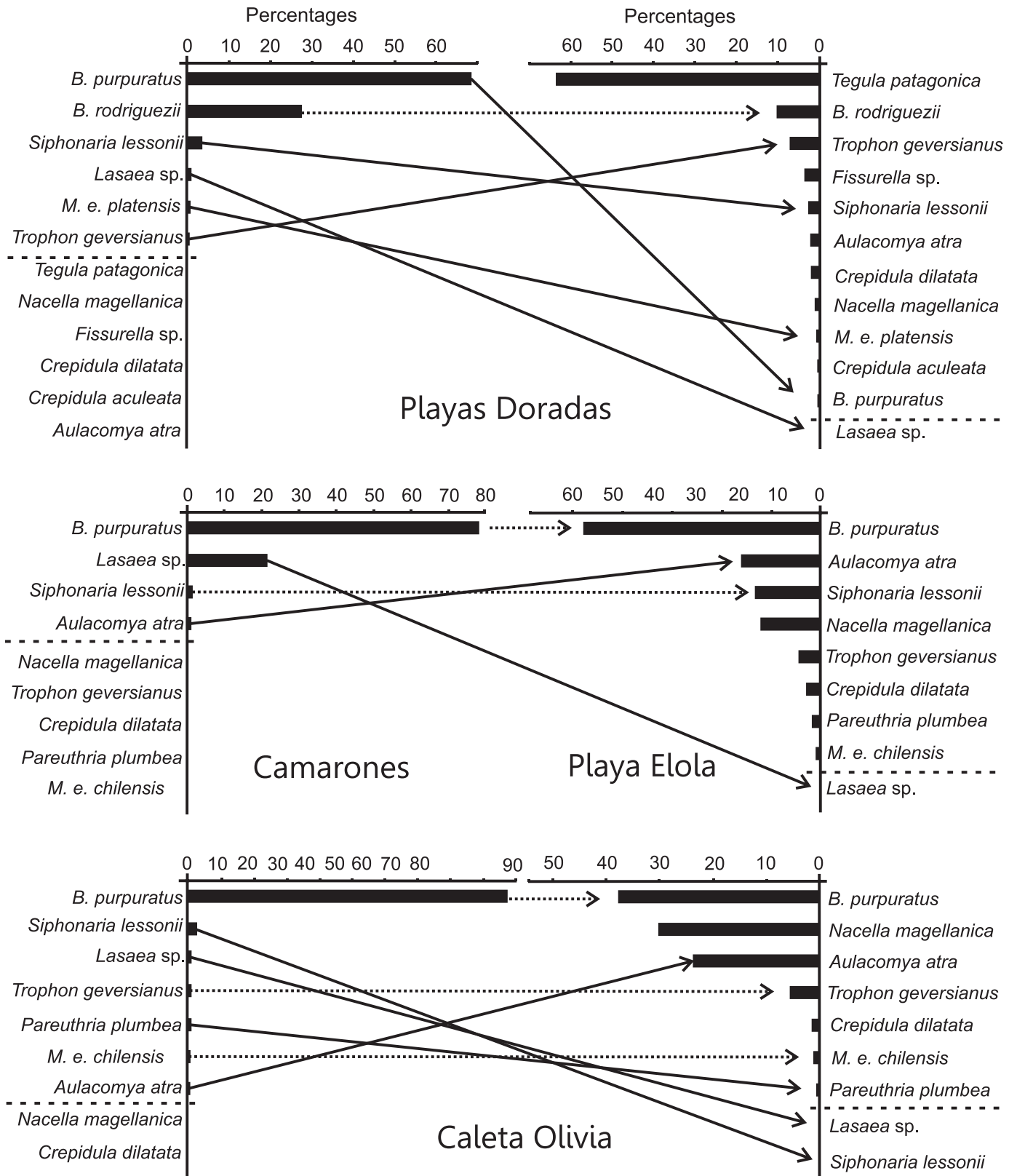*Pareuthria plumbea*
Lasaea sp.
Siphonaria lessonii

Fig. 6.—Bar plots with species-level composition of the living and death assemblages. Dissimilarities between LAs and DAs are reflected in differences in rank order and abundance of the taxa.
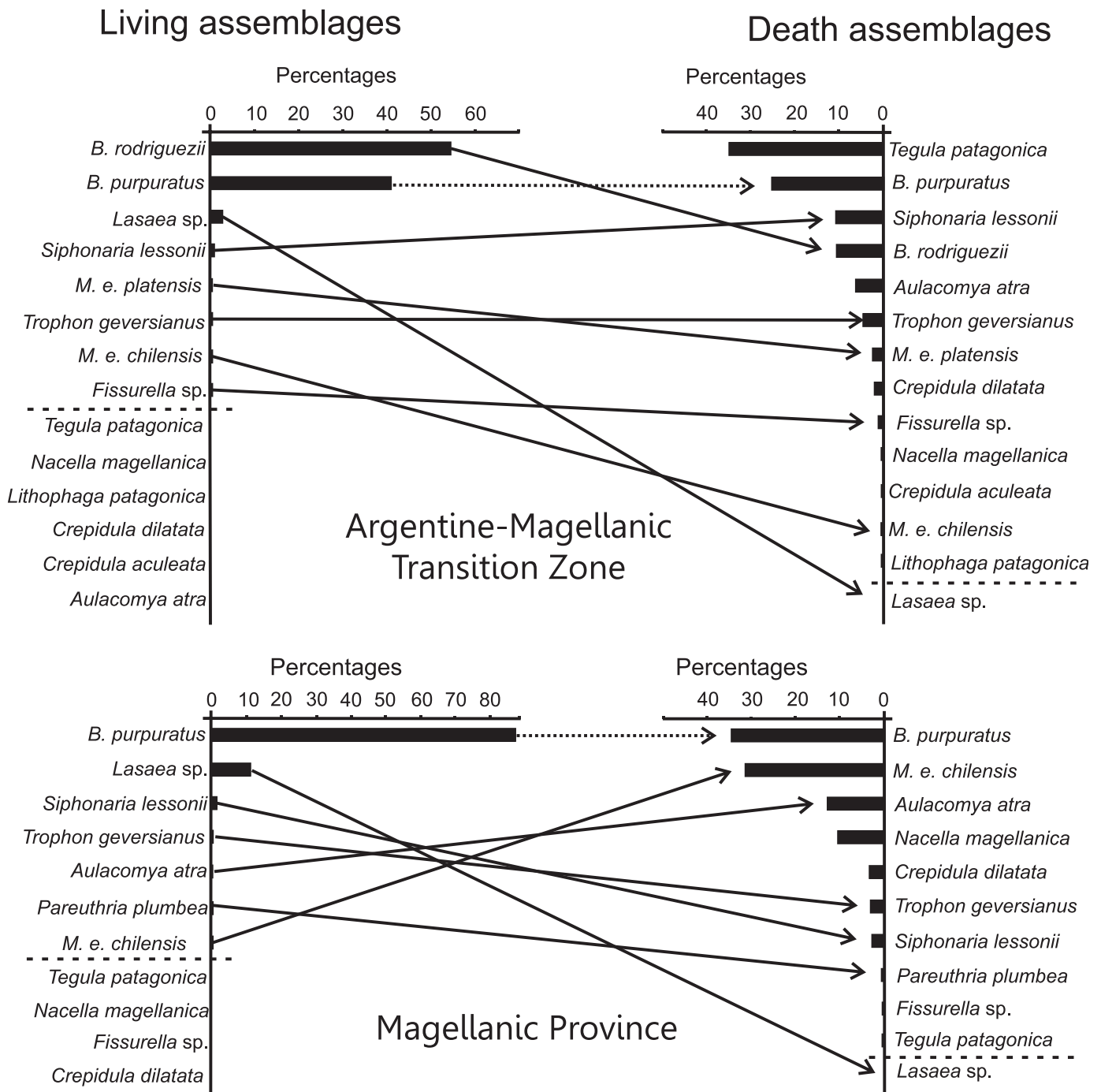
Living assemblages

Percentages
0 10 20 30 40 50 60

- B. rodriguezii
- B. purpuratus
- Lasaea sp.
- Siphonaria lessonii
- M. e. platensis
- Trophon geversianus
- M. e. chilensis
- Fissurella sp.
- - - - - - - - - - -
- Tegula patagonica
- Nacella magellanica
- Lithophaga patagonica
- Crepidula dilatata
- Crepidula aculeata
- Aulacomya atra

Death assemblages

Percentages
40 30 20 10 0

- Tegula patagonica
- B. purpuratus
- Siphonaria lessonii
- B. rodriguezii
- Aulacomya atra
- Trophon geversianus
- M. e. platensis
- Crepidula dilatata
- Fissurella sp.
- Nacella magellanica
- Crepidula aculeata
- M. e. chilensis
- Lithophaga patagonica
- - - - - - - - - - -
- Lasaea sp.

Argentine-Magellanic Transition Zone

Percentages
0 10 20 30 40 50 60 70 80

- B. purpuratus
- Lasaea sp.
- Siphonaria lessonii
- Trophon geversianus
- Aulacomya atra
- Pareuthria plumbea
- M. e. chilensis
- - - - - - - - - - -
- Tegula patagonica
- Nacella magellanica
- Fissurella sp.
- Crepidula dilatata

Percentages
40 30 20 10 0

- B. purpuratus
- M. e. chilensis
- Aulacomya atra
- Nacella magellanica
- Crepidula dilatata
- Trophon geversianus
- Siphonaria lessonii
- Pareuthria plumbea
- Fissurella sp.
- Tegula patagonica
- - - - - - - - - - -
- Lasaea sp.

Magellanic Province

FIG. 7.—Bar plots with species-level composition of the living and death assemblages for data pooled across samples per biogeographic region. Dissimilarities between LAs and DAs are reflected in differences in rank order and abundance of the taxa.

whereas juvenile individuals are present in all size-frequency distributions in LAs (Fig. 8). Also, histograms indicate that the rather complicated bimodal to multimodal distribution in LAs becomes unimodal (Fig. 8A–D) or platykurtic in DAs (Fig. 8E).

Therefore, the main bias between the LAs and DAs is probably size related. All samples come from communities living in the middle intertidal, and are thus subject to high water flows during high tides, which could be regulating the transport process toward the upper intertidal, at least for the small-sized shells. In the absence of burial in

rocky intertidal habitats and under reduced burial rates in mixed-bottom intertidal environments, juvenile specimens are also more likely destroyed than large-sized and thicker adults (Tomašových 2004).

The interpretation of a size-related bias is also supported by the observation that *Brachidontes* species are less frequent in DAs than in LAs. Mean per-sample percentages show that these small-sized mytilids represent almost 93% of the LAs and only 44% of the DAs. This underrepresentation of small-sized mytilids in DAs is consistent within each biogeographic unit. Therefore, the decrease in dominance of *Brachidontes* species could be
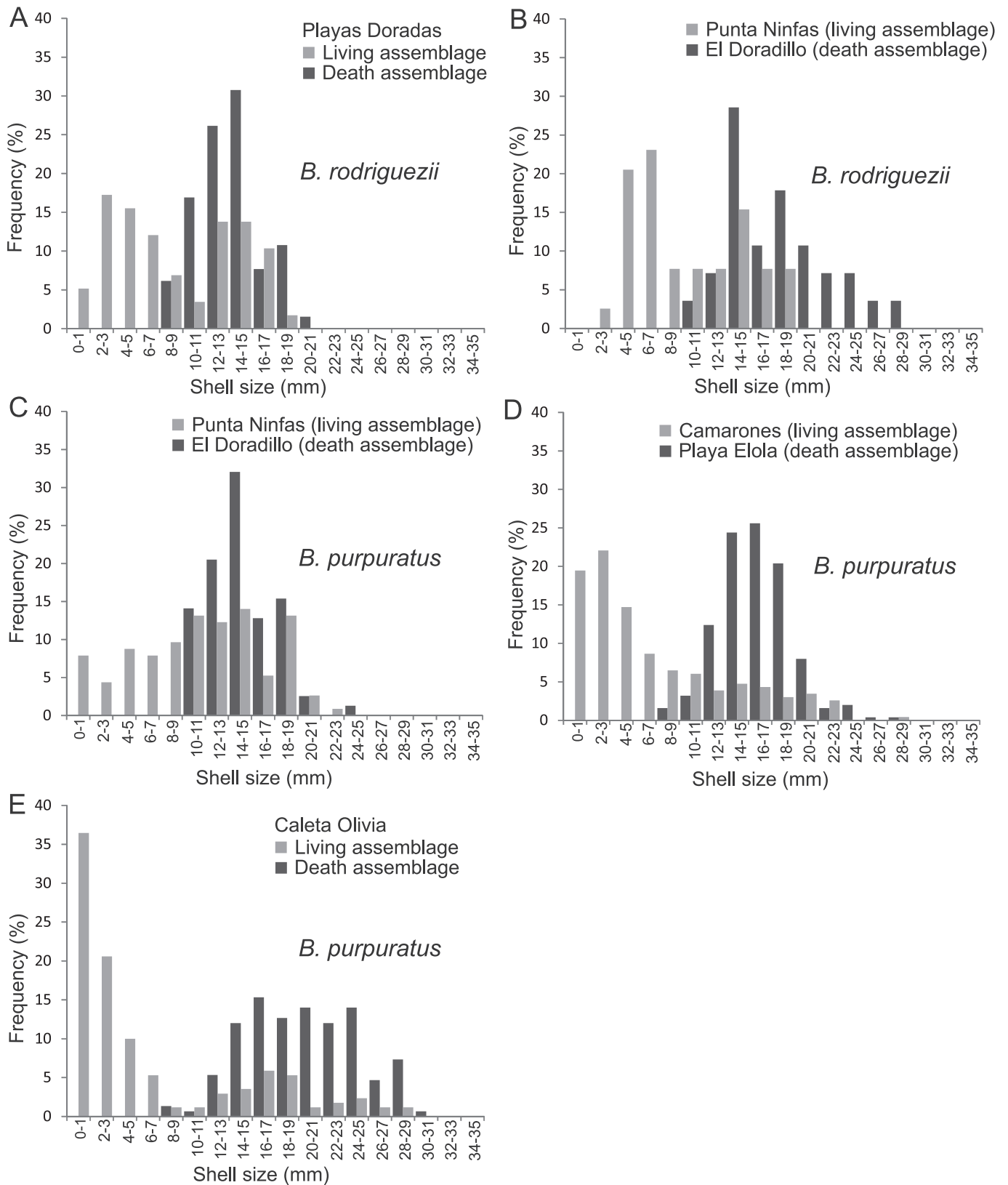
FIG. 8.—Size-frequency distributions of death assemblages are characterized by higher proportions of large-sized specimens with respect to specimens from living communities for *Brachidontes rodriguezii* and *B. purpuratus* at different localities. **A)** *Brachidontes rodriguezii*, Playas Doradas (LA vs. DA). **B)** *Brachidontes rodriguezii*, El Doradillo (DA) vs. Punta Ninfas (LA). **C)** *Brachidontes purpuratus*, El Doradillo (DA) vs. Punta Ninfas (LA). **D)** *Brachidontes purpuratus*, Playa Elola (DA) vs. Camarones (LA). **E)** *Brachidontes purpuratus*, Caleta Olivia (LA vs. DA). Symbols: black = specimens from death assemblages; gray = specimens from life assemblages.

Death assemblages   Living assemblages

■ *B. rodriguezii*
■ *B. purpuratus*

Argentine Province
Transition zone

1-Las Grutas

2-Punta Mejillón

3,4-Playas Doradas

42°

5-Puerto Lobos

7-El Doradillo

8-Puerto Madryn   6-Puerto Pirámides

Magellanic Province

9-Punta Ninfas

44°

10-Playa Elola

11-Camarones

12-Rada Tilly

46°

13,14-Caleta Olivia

15-Cabo Blanco

16-Puerto Deseado

48°

100 km
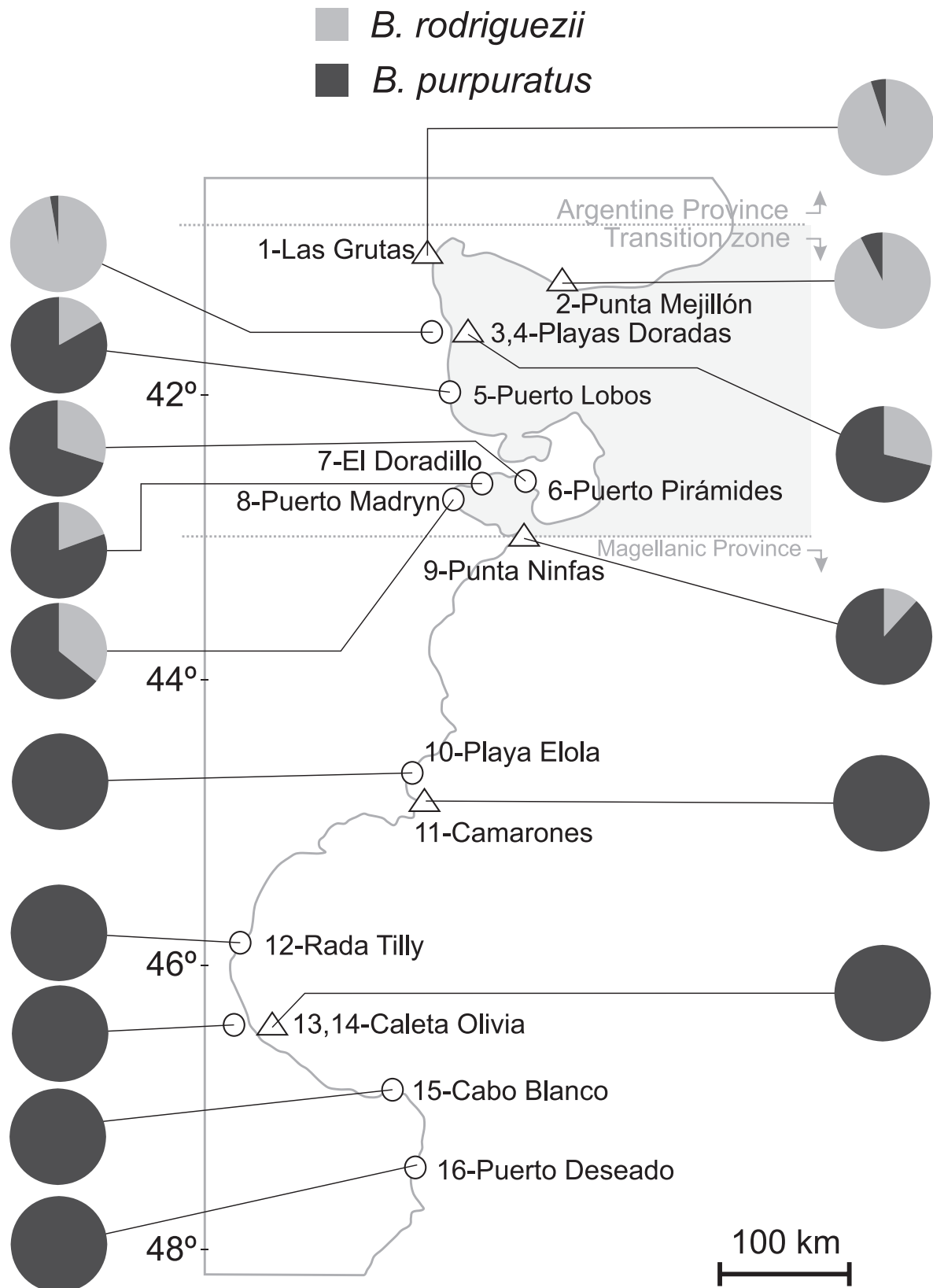
TABLE 5.— *Descriptive statistics of the sizes of* Brachidontes rodriguezii *and* B. purpuratus*, separated by locality and type of sample. Abbreviations: N = number of samples; CV = coefficient of variation.*

Brachidontes rodriguezii	PD_D	Lower conf.	Upper conf.	PD_L	Lower conf.	Upper conf.
N	65			58		
Mean	14.02	13.33	14.67	9.27	7.88	10.60
Variance	7.75	5.55	9.99	28.24	22.95	34.23
Median	14.02	13.38	14.58	8.05	3.50	10.12
25 percentile	12.19	11.15	13.72	4.60	3.28	6.08
75 percentile	15.77	14.26	16.82	14.05	12.32	15.41
CV	19.86	17.25	22.94	57.32	48.61	66.68

	ED/PN_D	Lower conf.	Upper conf.	ED/PN_L	Lower conf.	Upper conf.
N	28			39		
Mean	18.42	16.73	20.01	10.23	8.75	11.72
Variance	20.32	10.50	30.16	23.62	17.67	30.55
Median	17.87	15.55	20.69	8.36	3.56	9.68
25 percentile	14.47	12.10	14.81	6.23	5.01	7.58
75 percentile	21.11	17.86	23.99	14.57	12.86	17.96
CV	24.47	19.95	30.60	47.49	40.51	55.44

Brachidontes purpuratus

	ED/PN_D	Lower conf.	Upper conf.	ED/PN_L	Lower conf.	Upper conf.
N	77			114		
Mean	15.20	14.51	15.83	11.31	10.29	12.35
Variance	8.65	4.99	11.59	31.84	25.95	37.98
Median	14.91	14.12	15.65	11.55	9.79	12.94
25 percentile	13.09	12.19	13.94	6.93	4.95	8.86
75 percentile	16.64	14.76	17.35	15.50	13.36	16.73
CV	19.36	16.02	22.76	49.88	43.03	56.77

	PE/C_D	Lower conf.	Upper conf.	PE/C_L	Lower conf.	Upper conf.
N	250			230		
Mean	16.73	16.33	17.12	7.32	6.51	8.08
Variance	9.91	7.76	11.88	38.23	31.51	45.09
Median	16.66	16.19	17.22	5.26	4.53	6.26
25 percentile	14.52	14.03	14.87	2.30	2.03	2.60
75 percentile	18.65	18.05	19.20	10.74	8.45	12.82
CV	18.82	16.97	20.76	84.48	78.28	90.84

	CO_D	Lower conf.	Upper conf.	CO_L	Lower conf.	Upper conf.
N	150			170		
Mean	20.39	19.62	21.15	7.00	5.82	8.11
Variance	23.01	18.69	27.32	58.36	45.22	72.10
Median	20.35	19.09	21.39	2.91	1.62	3.39
25 percentile	16.71	15.66	17.62	1.62	1.49	1.90
75 percentile	24.34	23.71	25.51	12.56	9.10	18.83
CV	23.53	21.18	26.00	109.11	99.16	119.31

explained by the effect of destruction and transportation out of the habitat. Also, this decrease could alternatively be explained by the effect of time coarsening: DAs may combine the abundance structure of communities that changed dominant species through time (Tomašových and Kidwell 2010). Methodological differences in sampling collection between LAs and DAs might have partly contributed to the differences.

Effects of Temporal and Spatial Averaging on Species Diversity

The DAs studied here are inferred to be time averaged. A consequence of this process is the mixing of several generations in the same environment (Fürsich and Aberhan 1990; Tomašových and Kidwell 2009; Kidwell and Tomašových 2013). Higher levels of species richness and evenness coincide with the prediction of increased diversity in DAs (Fürsich and Aberhan 1990; Tomašových and Kidwell 2010; Kidwell and Tomašových 2013). The reduction in dominance and enrichment in rare species has also been identified as a likely result of time averaging because as the time during which a DA receives hard parts increases, the probability of incorporation of new species by immigration of nearby locations and/or the occurrences of changes in habitat conditions (e.g., varying proportions of soft- and hard-bottom patches in intertidal environments) also increases (Fürsich and Aberhan 1990; Tomašových

←

FIG. 9.—Proportions of *Brachidontes rodriguezii* (light gray) and *B. purpuratus* (dark gray) across the studied area show that both living and death assemblages capture the latitudinal gradients in their abundance. Symbols: circles = death assemblages; triangles = living assemblages.

and Kidwell 2010; Kidwell and Tomašových 2013), although similar effects can be produced by spatial mixing.

Calyptraeid species, true limpets, and large mytilids, which are absent or scarce in LAs but present and in some cases abundant in DAs, are typical of lower intertidal to subtidal environments and rarely occur alive in middle intertidal rocky habitats (Olivier et al. 1966b; Zaixso and Pastor 1977; Bertness et al. 2006; Silliman et al. 2011). Similarly, the mismatch in abundance of the snail *Tegula patagonica*, which reaches high abundance in DAs (1,885 individuals in Puerto Madryn) but does not occur in LAs (and is considered a rare inhabitant of the mid-intertidal rocky habitat; Sánchez and Zaixso 1995; Wieters et al. 2012), is another example of a species that is rare in the LAs and becomes common in the DAs. All these species that are absent or rare in LAs, but present and sometimes abundant in DAs, correspond to rare inhabitants of the middle intertidal that were incorporated in disproportionately higher abundance due to the temporal coarsening or spatial mixing of these samples.

Spatial Variation in Composition at Biogeographic Scales

The species composition and abundance of LAs vary along a latitudinal gradient (Fig. 5), following a poleward decrease in seawater temperature. On one hand, this latitudinal pattern is not present among DAs within the same biogeographic unit. On the other hand, compositional differences between the Transition Zone and Magellanic Province are still clearly captured by DAs. The latitudinal gradient captured by LAs coincides with a gradual replacement of *Brachidontes rodriguezii* (species characteristic of the Argentine Biogeographic Province) by *B. purpuratus* (typical of the Magellanic Biogeographic Province) (Fig. 9). In contrast, DAs in the Transition Zone are characterized by a relatively stable percentage of both *Brachidontes* species (sites 5 to 8), with the exception of Playas Doradas which has a small proportion of *B. purpuratus* (Fig. 9). Spearman rank correlation between latitude and logarithm of the ratio of *B. rodriguezii* to *B. purpuratus* in the Transition Zone showed a negative correlation in the case of LAs (rs = –1, p = 0.083) that is however nonsignificant, and a weak and nonsignificant correlation in the case of the DAs (rs = –0.1, p = 0.783). Mussel beds in the Transition Zone show high heterogeneity (patchy distribution) with respect to the proportion of both *Brachidontes* species (Arribas et al. 2013), a pattern that does not help in explaining the lack of gradual replacement in DAs. However, the increase in *Brachidontes rodriguezii* from the Magellanic toward the Transition zones contributes to the between-province separation in the DAs. The temporal changes in community structure of LAs at the contact between the Magellanic and Argentine Biogeographic Provinces likely produced a mix of shells from both provinces with variable proportions, but was not enough to homogenize of the two biogeographic zones

Boretto et al. (2013) detected temporal changes in the molluscan species composition during the Quaternary along the Puerto Lobos coastal area. These authors compared the Pleistocene, Holocene, and Modern fauna. The presence of *Tegula atra* and *Mactra patagonica* in Pleistocene sediments indicated a greater proportion of taxa typical from the cold-water Magellanic Province; however, during the Holocene the most typical element in the area was *Glycymeris longior,* characteristic of the Argentinean Province. During the late Holocene, this study area also recorded a faunal shift in which species belonging to the Magellanic Province displaced the fauna of the Argentinean Province to the north, probably in coincidence with the Little Ice Age.

The presence of *B. rodriguezii* in the study area can be traced back to the Miocene Paraná and Madryn Formations of Argentina and Uruguay (del Río and Martínez 1998). *Brachidontes purpuratus*, in turn, seems to be a more recent immigrant from the southeastern Pacific (during

Plio–Pleistocene transition) based on genetic, morphological, and geological evidence (Trovant et al. 2013, 2015). Trovant et al. (2015) suggest that the distribution of *B. purpuratus* is related to latitudinal gradients in the sea surface temperature (*B. purpuratus* favors SST below 13 °C), although its expansion northward is probably blocked by the high densities of *B. rodriguezii*. In this way, climatic fluctuations in the last few hundreds or thousands or years may have pushed the Transition Zone northward or southward and then blurred the pattern of gradual replacement between species in the DAs. Possible temporal changes in the distribution of these species may also help explain the low association in rank abundance between adjacent localities observed in this study (Fig. 6, upper part). This observation is reflected in the statistically significant differences between LAs and DAs in the Transition Zone (seen in PERMANOVA results).

This result coincides with those of Tomašových and Kidwell (2009) where the variability in species composition among DAs is lower than among LAs for both abundance and presence-absence data. It is possible that the time involved in the formation of DAs caused mixing in the species composition of the communities due to ecological succession, immigration, extinction, or due to stochastic and environmental changes (Fürsich and Aberhan 1990; Bennington 2003; Tomašových and Kidwell 2009), leading to the lack of latitudinal gradient in composition of DAs within provinces. However, the possible homogenization generated by those mechanisms was not sufficient to reduce differences between the Argentine-Magellanic Transition Zone and the Magellanic Province.

CONCLUSIONS

1. Death assemblages from intertidal rocky shores on the Atlantic coast of Patagonia show a moderate agreement in species composition and abundance between DAs sampled in mixed-bottom intertidal environments and living mussel communities inhabiting nondepositional rocky bottoms in the same region. Even when spatial variation within the two provinces seems to be homogenized (probably due to the averaging of successive communities affected by fluctuating temporal changes in the biota), differences between the Argentine-Magellanic Transition Zone and the Magellanic Province are clearly detected in DAs. Our results reinforce the usefulness of death assemblages as proxies of living communities at regional spatial scale (Kidwell and Tomašových 2013) and justify the reliability of studies based on them (e.g., Gordillo and Archuby 2012, 2014; Martinelli et al. 2013).

2. Death assemblages have higher diversity than living assemblages, probably due to their time-averaged nature (and spatial mixing).

3. The main taphonomic distortion between LAs and DAs is the lower abundance of small species and the underrepresentation of smallest specimens (less than 8 mm). This bias is probably caused by differential transport and destruction by waves, currents, and wind. Another source of live-dead mismatch seems to be related to reduced detectability of vagile epifaunal species and boring species in LAs.

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