



# Pleistocene and Holocene interglacial molluscan assemblages from Patagonian and Bonaerensian littoral (Argentina, SW Atlantic): Palaeobiodiversity and palaeobiogeography

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## ABSTRACT

Our analysis of palaeobiodiversity and palaeobiogeography of Quaternary molluscan assemblages provide information on the last coastal scenarios in the SW Atlantic. We present patterns of species richness, areas of endemism and between areas relationships based on records (721 taxa) from Argentina and northwards in South America (Surinam, Brazil, Uruguay), including Pleistocene, Holocene and modern sites (48 localities). In Argentina, our data since the Mid-Late Pleistocene (MIS11-1; ca. 400 ka B.P. to present) suggest environmental changes linked to sea-level and climatic fluctuations, large enough to alter benthic associations (compositional, geographical variations, including a few extinctions). The southwards decreasing diversity trend for modern bivalves (mostly infaunal taxa) and gastropods (mostly epifaunal taxa), from Surinam to Tierra del Fuego, responds mainly to latitudinal SST, salinity barriers, hydrodynamic forces (rivers and shallow currents): minima peaks fit with local estuarine and marginal marine sites influenced by the Río de la Plata plume; highest peaks with fully marine, warmer waters influenced by the Brazilian Current (Bonaerensian sector); a similar trend applies for the Holocene; Pleistocene maxima peaks in Patagonia belong to MIS11 and MIS5 highstands (warmer than today). Multivariate (Cluster Analysis, CA; Minimum Spanning Trees superimposed to Principal Coordinates Analysis, PCO) and cladistic (Parsimony Analysis of Endemism, PAE) methods showed congruent relationships between localities, discriminating marginal from open marine environments, but PCO combined with PAE was most advantageous for our area and dataset (382 gastropods, 339 bivalves; 29 Pleistocene, 28 Holocene and 35 modern sites) allowing objective, quick comparisons. Shifts of areas of endemism during the Holocene and Pleistocene relate with SST and salinity changes; a more homogeneous Mid-Holocene (ca. 7–5 ka B.P.) scenario, of regionally increased salinity and higher (ca. 2 °C) SST, defined the Bonaerensian and northern Patagonian sectors, facilitating southwards shifts of bivalve and gastropod taxa; for Patagonia a colder Pleistocene scenario south of SAO is documented by *Tegula atra* (exclusive Pleistocene cold water species extinct in the SWA), probably a signal of post-LGM palaeoceanographical changes in the Mar Argentino.

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## 1. Introduction

In this contribution, based on marine molluscan records of Late Pleistocene, Holocene and modern age along Argentina (SW Atlantic margin), we search for information on diversity patterns, areas of endemism and their eventual changes through time, adding comparisons with other littoral settings of South America. We attempt to identify probable biotic responses to environmental/climatic factors.

In the marine realm much still needs to be investigated concerning the distribution of taxonomic groups in space and time. Estimations of Quaternary marine palaeobiodiversity and palaeobiogeography represent one of the tasks for a better understanding of the effects of the last climatic cycles on oceanic life. For the Quaternary, characterized by a stable tectonic scenario, plausible explanations for geographic patterns rely on individual dispersal abilities and/or vicariance linked to environmental changes produced as a consequence of such cycles, both leading to present-day geographic arrangements (Allmon et al., 1993; Jablonski, 2008; Valentine et al., 2008; Miller et al., 2009; Roy et al., 2009; other references therein). On the other hand, large-scale patterns of species richness are one of the ongoing cornerstones of macroecological research (Borregaard and Rahbeck, 2010) and need to be improved for benthic littoral marine groups.

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Benthic molluscs play a major role in nearshore environments where they are highly diverse today and a predominant biogenic component of Neogene littoral deposits. While their present-day diversity gradients have been intensively studied in different regions of the world (Jablonski et al., 2000, 2006; Roy et al., 2000; Rex et al., 2005; Smith and McGowan, 2007; Crampton et al., 2010; references therein), research data on the Southern Hemisphere are scarce and geographically incomplete (Rivadeneira et al., 2002; Valdovinos et al., 2003, 2008; Fortes and Absalão, 2004; Benkendorfer and Soares-Gomes, 2009). One exception to this general pattern is, however, the Southern Ocean (Antarctica and Sub-Antarctic islands) where recent studies significantly advanced in our knowledge of extant diversity in this and related groups (Linse, 1999; Troncoso et al., 2001; Linse et al., 2006; Barnes and Griffiths, 2007; Clarke et al., 2007; Griffiths et al., 2009; Barnes and Hillenbrand, 2010). Available data about Quaternary molluscan assemblages refer mainly to Australia (Murray-Wallace et al., 2000), New Zealand (Beu et al., 1997; Beu, 2009), Chile (Ortlieb et al., 1996a; Rivadeneira and Carmona, 2008; Rivadeneira et al., 2011; Kiel and Nielsen, 2010; Perú (Ortlieb et al., 1996b); Argentina (Aguirre et al., 2009), Magellan region and Beagle Channel (Cárdenas and Gordillo, 2009); Magellan-Antarctic area and southern high latitude connections (Arntz et al., 2005). For Atlantic South America, however, they are still insufficiently known.

Our own sampling of the Quaternary molluscan assemblages from Argentina between the Río de La Plata margin and southern Santa Cruz province is now reasonably complete and extensive, allowing us to attempt an analysis of palaeobiodiversity and palaeobiogeography since the Pleistocene based on a large and updated dataset, including comparisons based on compilations through an exhaustive search of primary literature and systematic bibliography from other coastal areas of the Southwestern Atlantic (Surinam, Brazil, Uruguay) (Fig. 1a, b) (see electronic appendixes S1, S2a, S2b).

We attempt to address: 1) if there is a geographic pattern of biodiversity (species richness) for the marine Quaternary of Argentina (coastal area of Patagonia and Buenos Aires province, here called Bonaerensian sector) through time, at least since the Middle-Late Pleistocene (to fill the SWA gap concerning biodiversity of nearshore molluscs, adding new data to the discussion about marine latitudinal trends being valid worldwide or only applicable to epifaunal taxa from low and temperate oceanic latitudes); 2) if it is possible to recognize areas of endemism (areas characterized by a non random distributional congruence of two or more taxa; sensu Morrone, 1994) and if they varied in space and time in our area; 3) if patterns between areas/localities, defined through multivariate methods, can be interpreted as responses of Quaternary marine molluscs to climatic/abiotic controls and palaeoenvironmental and palaeoclimatic changes; 4) to compare results by multivariate and cladistic methods to assess these approaches and if there is any more advantageous method to deal with these problems in the study area.

Assuming that biodiversity is a result of the history of life on Earth expressed through changes of form in space and time (Crisci et al., 2003) and that life varies non-randomly geographically and through time (Stanley, 1997; Lieberman, 2003, 2005), these approaches have direct implications in deciphering littoral marine biotic responses to the last climatic changes.

According to this, we hypothesize that: 1) the cyclic Pleistocene–Holocene climatic variations caused environmental changes along the littoral area of Argentina, mainly in terms of salinity and sea surface temperature (SST) controlled by continental runoff, winds and shallow oceanic currents; which were large enough to alter molluscan biodiversity and/or geographic ranges; 2) they may have affected both gastropods and bivalves, although not necessarily in an identical way. Alternatively, the littoral molluscs may not have varied in terms of biodiversity or geographic patterns due to the lack of sufficiently important environmental changes occurred to present.

Our results can reduce the unbalanced framework for diversity patterns worldwide as most published data outcome from the

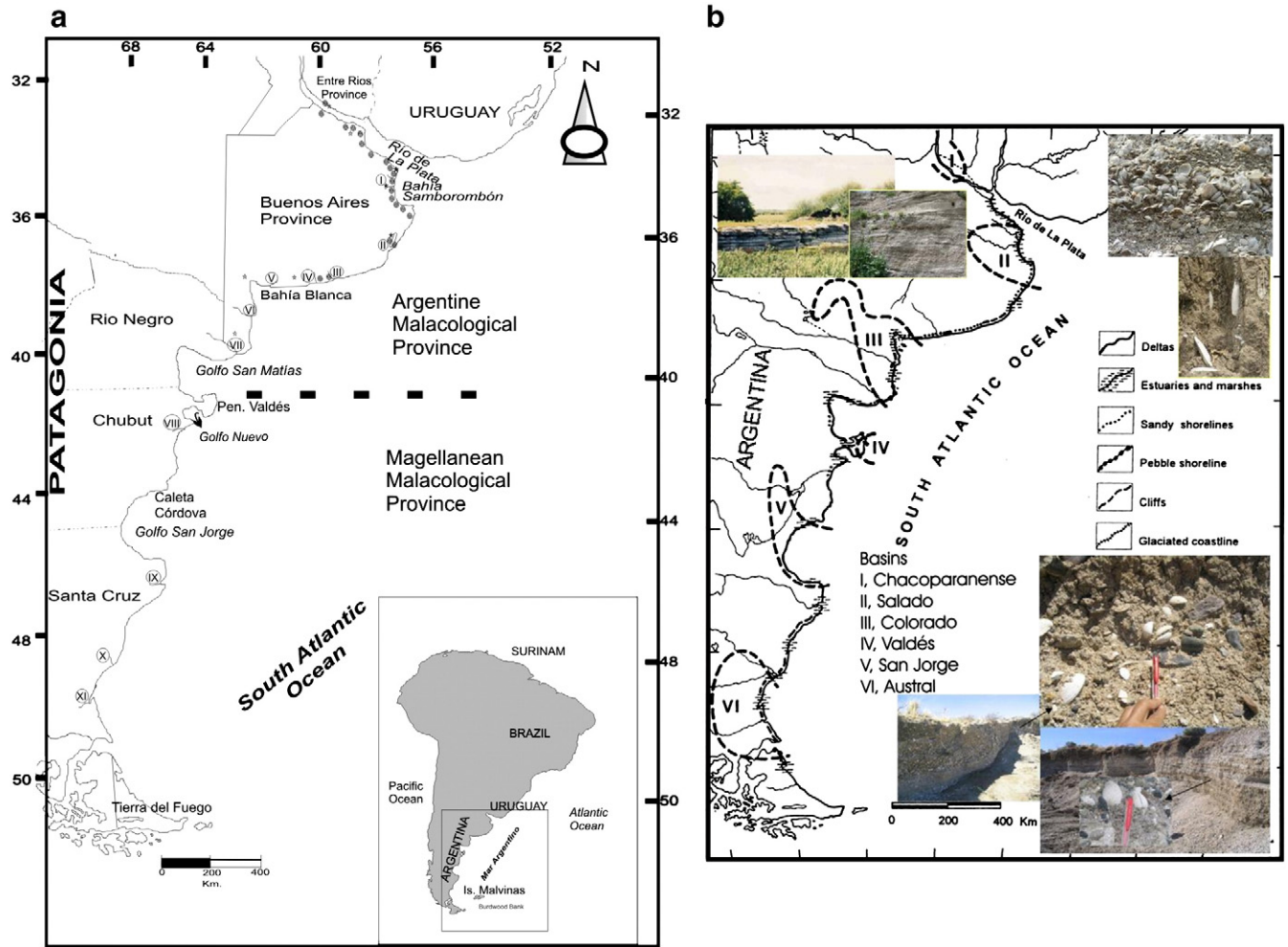
Northern Hemisphere and terrestrial records. Also, they can add to the still in progress scientific debate regarding the validity of a global geographic marine biodiversity trend. Finally, a wide variety of Quaternary palaeoenvironmental evidence linked to palaeoclimate changes are available for Argentina (references in S2b), but most relate to continental records while contributions based on invertebrates and on marine taxa are comparatively scarcer.

To afford a synthesis of molluscan diversity and biogeographic patterns since the Pleistocene to present in our area is of primary importance to add in our understanding of biotic responses of benthic littoral faunas to Quaternary climatic cycles in the Southern Hemisphere. In turn, molluscan records showing these responses can represent a useful tool in future studies to interpret taxonomic/evolutionary patterns linked to environmental changes during the most recent past and for phylogeographic research. Especially the coastal area of Patagonia can be looked at as a natural laboratory, far from human impacts, to search for climatic effects as a model of probable future climate change influence on coastal marine life (Fields et al., 1993; Warwick and Turk, 2002). This source of evidence from our area is fundamental to establish palaeoenvironmental comparisons with other coastal areas worldwide.

## 2. Geological setting and previous studies

The last Neogene transgressions along the Southwestern Atlantic margin in South America are well testified by sedimentary records with molluscan concentrations originated during high sea-level stands in the Late Miocene (ca. 10 Ma B.P.), Pliocene (scarce distribution, unknown ages), Pleistocene (since at least 400 ka B.P. to 125 ka B.P.) and mid-Holocene (maximum ca. 8–5 ka B.P.). The cycles are correlated with the marine isotopic stages stratigraphy. In Argentina, Quaternary molluscan assemblages are abundant and well preserved along the coastal area between the Río de La Plata margin and southern Patagonia (Fig. 1a, b; S1). The richest and thickest skeletal accumulations, comprising mainly gastropod and bivalve shells, are parautochthonous (sensu Kidwell, 1986) and originated during the last transgressive-regressive Mid-Late Pleistocene and Holocene marine cycles, known as Marine Isotope Stages (MIS) (Burckle, 1993; Winnograd et al., 1997; Zachos et al., 2001; S2a). Along Patagonia (Río Negro, Chubut and Santa Cruz provinces) these skeletal accumulations integrate beach ridges, marine terraces and estuarine deposits derived from at least four Pleistocene high sea-level episodes, MIS11 (ca. 400 ka), 9 (ca. 325 ka), 7 (ca. 225 ka), 5e (ca. 125 ka) and the last one during the Holocene (MIS1, present day) (e.g., Feruglio, 1950; Codignotto et al., 1988; Rutter et al., 1989, 1990; Rostami et al., 2000; Schellmann and Radtke, 2000, 2003; Schellmann, 2007). Northwards along the Bonaerensian coastal area they are arranged within beach ridges, tidal flats and coastal lagoonal facies, mostly resulting from the Last Interglacial (MIS5e) and the post Last Glacial Maximum transgression (MIS1) (Aguirre and Whatley, 1995).

Our knowledge on these assemblages and of the modern molluscan counterparts living in the adjacent littoral (Mar Argentino) goes back to taxonomic lists in reports of historical expeditions along the Argentine pampas and Patagonia and to the classical monographic contributions since the nineteenth century. In addition, inventories of taxa recovered by oceanographic expeditions, especially during the twentieth century, are available for wide areas of the Argentine continental shelf even when the collection stations are generally restricted (following a patchy pattern as they were aimed mainly at fishery exploration purposes) (S2). Various systematic, taphonomic (post-mortem history leading to preservation in the final depositional environment), qualitative and quantitative molluscan studies have more recently been produced for the marine Quaternary in several Patagonian and Bonaerensian coastal sectors (see Aguirre et al., 2008 and other references in S2b). These studies can be used to compare or complement compositional, palaeoenvironmental or geological



**Fig. 1.** Area of study in South America (SW Atlantic margin). a. Modern biogeographic regions (Argentine and Magellanean Malacological provinces). Main rivers mentioned in the text: I, Río Salado, Río Samborombón; II, Laguna Mar Chiquita; III, Río Quequén Grande; IV, Río Quequén Salado; V, Río Sauce Grande; VI, Río Colorado; VII, Río Negro; VIII, Río Chubut; IX, Río Deseado; X, Río Santa Cruz; XI, Río Coy (Coyle). Symbols show the spatial distribution of Holocene and Pleistocene marine deposits (beach ridges, tidal flats, coastal lagoons) (not in scale). Along the text, Río de la Plata as RLP, Golfo San Matías as GSM. b. Sedimentary basins and littoral landforms along the coast of different areas of Argentina. Modified from Codignotto et al. (1992; other references therein) and Clapperton (1993). Examples of Late Pleistocene and Holocene molluscan shell concentrations considered for palaeodiversity and palaeobiogeographic analyses. Typical coastal deposits at the Bonaerensian (shell ridges, tidal flats) and Patagonian (marine terraces) sectors. Complete joined valves in life position of *Tagelus plebeius* (Lightfoot) (Bonaerensian area) and *Protothaca antiqua* (King) (Patagonia).

characterizations linked to different marine episodes as established by the global isotope curve (Haq et al., 1987). Specifically, palaeobiodiversity and palaeobiogeography represent target missing points and a gap in our knowledge of the littoral marine scenarios for this geographic area of the Southern Hemisphere, time span (MIS11-1) and taxonomic groups (bivalves and gastropods).

**3. Study area**

Our study provides comparisons between several coastal areas of South America along the SW Atlantic margin (SWA) but is centered on Argentina (Fig. 1a, S1). The Argentine region analyzed, provided with own personal collections, comprises the area extending between the Río de La Plata (RLP) margin in the north and south of Puerto Coig surroundings in the south. It includes the Río Negro, Chubut and Santa Cruz provinces in Patagonia and the Bonaerensian area northwards. In addition, we considered information gathered from museum collections, bibliographic sources and oceanographic expeditions in the Mar Argentino (Argentine Sea) and SWA.

In the coastal sector of Argentina, placed at a passive tectonic margin with an extensive continental shelf, the innermost boundaries of successive Quaternary high sea-level episodes reached further

inland around sedimentary basins: Austral, San Jorge, Valdés, Colorado, Salado, Chaco-Paranense (Fig. 1b). The majority and the richest shell concentrations are most frequently preserved along wide bays, gulfs, coastal lagoons and river outlets (e.g., in Patagonia: Río Coig (Coyle), Río Santa Cruz, Río Deseado, Golfo San Jorge (GSJ), Río Chubut, Golfo Nuevo, Golfo San Matías (GSM), Río Negro; northwards in the Bonaerensian area: Río Colorado, Bahía Blanca, Río Sauce Grande, Río Quequén Salado, Río Quequén Grande, Laguna Mar Chiquita, Bahía Samborombón, Río Salado, Río Samborombón, RLP) (Fig. 1a).

**3.1. Fossiliferous deposits studied**

Quaternary molluscan concentrations extend almost continuously in the coastal area of Argentina from the modern supratidal zone to a few kilometers inland, reaching a maximum of ca. 20/30 km in some regions (e.g., south of Bahía Samborombón) but generally ca. 5–10 km (Camarones, Bahía Bustamante surroundings). Most of the fossiliferous deposits were accumulated during the Holocene (MIS1) and Mid-Late Pleistocene (MIS5e to 11) of which the most continuous and richest belong to MIS1, 5e and 7. The best preserved shells belong to MIS1 and MIS5e. Earlier highstands (pre-MIS11) may have been

preserved further inland, but the molluscan content, at least superficially, is either scarce and highly abraded or completely unpreserved.

The molluscan shells conform in general parautochthonous assemblages (sensu Kidwell et al., 1986), where extensive biostratigraphic and diagenetic bias of the shells can be excluded (Aberhan and Fürsich, 1991). Exceptionally, scarce, very well preserved autochthonous individual shells can be found in restricted Pleistocene or Holocene levels, within predominantly fine sediments of low energetic facies (e.g., in the Bonaerian deposits, complete bivalves in life position of *Tagelus plebeius* and less frequently of *Mactra isabelleana*, *Corbula patagonica*, *Macoma uruguayensis*, *Abra aequalis*; in deposits from Patagonia, of *Protothaca antiqua* and more rarely of *Mytilus edulis*, *Brachidontes* spp., *Ensis macha*, *Macoma* sp. (see S4)).

Gastropod shells show, in general, more abraded surfaces with greater loss of their original color and luster, except for *Tegula atra* (Lesson) within the Pleistocene Patagonian marine terraces. Bivalves, commonly better preserved, are assumed to offer higher palaeoecological value and more reliability in terms of palaeoenvironmental, palaeodiversity and palaeobiogeographic approaches. According to palaeoecological studies performed previously in many areas of the whole Argentine coast, it is assumed that the original molluscan communities must have lived in varied substrates of neritic waters, within the supralittoral, intertidal and upper infralittoral zones down to approximately 100 m deep (Aguirre et al., 2009, 2011).

Due to their young age, high preservation grade and similarity (taxonomic fidelity) of the Pleistocene and Holocene molluscan assemblages regarding the present-day nearshore associations, they are ideal for palaeoenvironmental and palaeobiogeographic analysis. On top of that, as they are time-averaged, the assemblages sampled can record long-term conditions of the depositional littoral environments (Aberhan and Fürsich, 1991).

Illustrations of the molluscan taxa identified can be found in previous papers dealing with different coastal areas of Argentina (Feruglio, 1933; Aguirre, 1993a, 2003; Aguirre and Farinati, 2000; Aguirre et al., 2005, 2006, 2007, 2008, 2009) (see also S2b, S4).

The deposits sampled in Argentina can be correlated with approximately synchronous shelly accumulations preserved in nearby coastal areas of Atlantic South America (Surinam, southern Brazil and Uruguay). Sources of information for morphostratigraphy, sedimentology, age, geological aspects of the deposits sampled and specific information on molluscan systematics, palaeoecology and distribution were published elsewhere, including detailed information on complete species lists and stratigraphic and geographic ranges (S2a, S2b).

### 3.2. Modern littoral

Basic information concerning the main physical features of the Mar Argentino, fundamental to our understanding of diversity and biogeographic patterns of the molluscan fauna analyzed, is synthesized in Fig. 2a, b. Biogeographic relationships of the Argentine benthic fauna and the boundaries for the regions identified on the basis of different taxa (which can vary according to the taxonomic groups considered) are strongly linked firstly, to sea surface temperature (SST) resulting from atmospheric-circulation patterns, and also to other abiotic factors (substrate nature, salinity, light, water movement, apart from dissolved nutrients and oxygen availability).

The Mar Argentino extends between the Río de La Plata-Paraná Delta and Tierra del Fuego where the Argentine coast comprises ca. 5.700 km with a NE-SW orientation (Fig. 1). Mean SST in the SW Atlantic varies from ca. 6 to 24 °C in summer (January) and ca. 2–18 °C in winter (July) (Hoffmann et al., 1997). Along the Southwestern Atlantic Shelf (SWAS) (55°S–23°S; Cabo Frío, Brazil, to Burdwood Bank) which represents the largest continental shelf of the Southern Hemisphere (Palma et al., 2008), the Argentine continental shelf (34°S–55°S) exhibits the widest and of more gentle relief worldwide. It is characterized by waters mainly of subantarctic origin through the

Drake Passage and Malvinas (Falkland) current, modified by local prevailing winds, temperate thermal cycle and weakened through dilution by coastal inputs. The freshwater balance, on the other hand, results from continental runoff (from the Fuegian channels, Magellan Strait, and several rivers northwards) as well as from evaporation–precipitation rates (e.g., Boltovskoy et al., 1999; Bogazzi et al., 2005; Lucas et al., 2005; Boltovskoy, 2007) (see S2c).

Along the Mar Argentino four salinity fronts and three thermal fronts are relevant to our study area (Fig. 2b, 2). Two modern malacological provinces can be recognized: Argentine and Magellanean (Fig. 1a). Detailed information on the main physical features of the Argentine continental shelf is available through studies from different standpoints published elsewhere (e.g., Acha et al., 2004, 2008; Piola et al., 2005, 2008, 2010; Romero et al., 2006; Boltovskoy, 2007; Balech and Ehrlich, 2008; Palma et al., 2008; Oliveira et al., 2009; Papparazzo et al., 2010; see S2c).

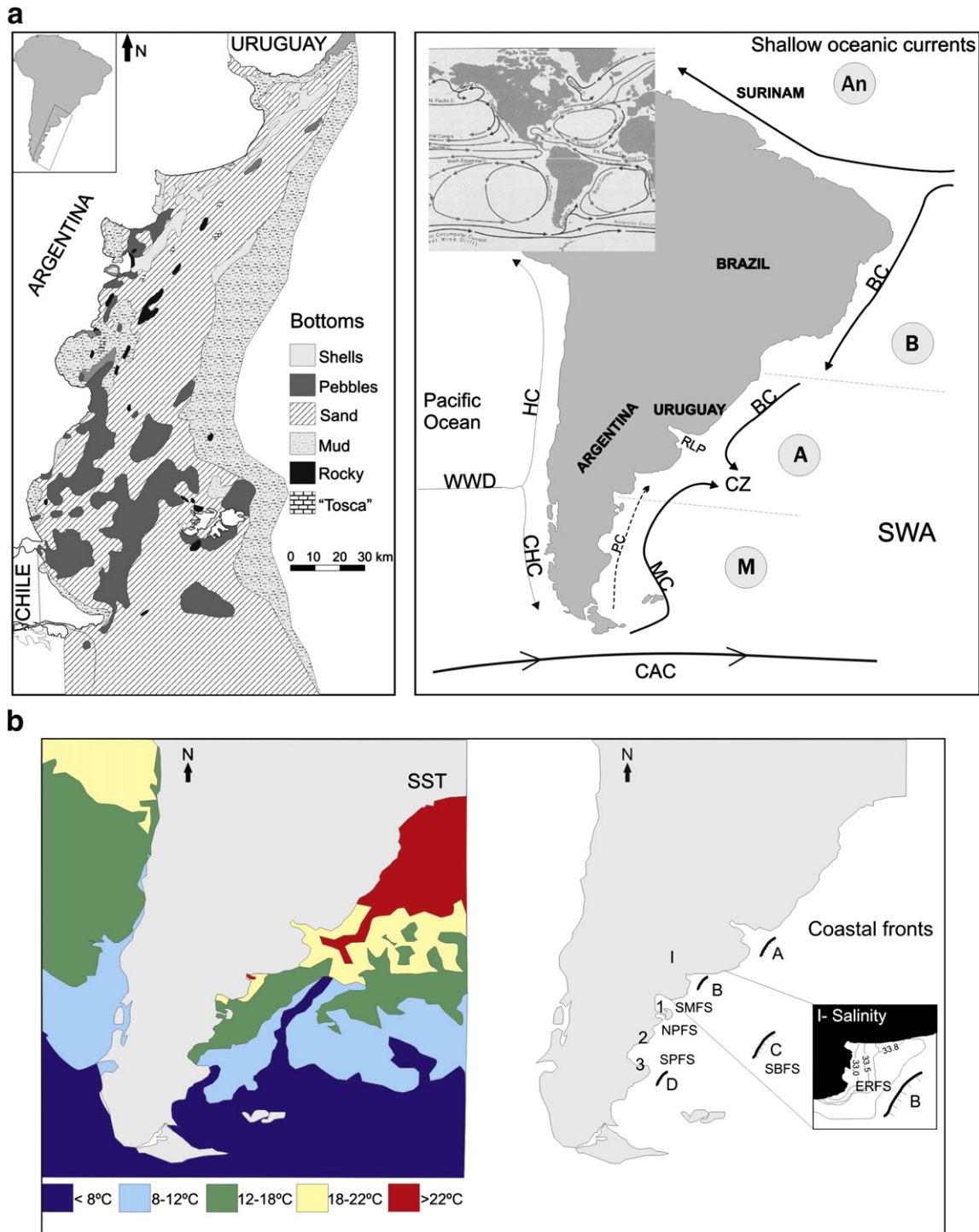
## 4. Material and methods

The material studied comes from shore surveys, field observations and sampling: own fossil and modern samples collected between 1982 and 2010 (published and unpublished data) along the Argentine coastal area (between ca. 35°S and 48°S), fossil and modern samples examined from museum and institutional collections (MACN: Museo Argentino de Ciencias Naturales at Buenos Aires; MLP: Museo de La Plata; BMNH: Natural History Museum, London; INIDEP: Instituto Nacional de Investigación y Desarrollo Pesquero at Mar del Plata). Additionally, we considered fossil and modern records from bibliographic sources (Surinam, Brazil and Uruguay; Tierra del Fuego) including data from oceanographic expeditions along the Mar Argentino (e.g., Carcelles, 1944, 1950; Richards and Craig, 1963; Castellanos, 1967; Scarabino et al., 1975; Scarabino, 1977; Zaixso et al., 1978; Castellanos and Landoni, 1988–1993; Lopez Gappa et al., 1993; Bastida et al., 2007; Giberto et al., 2007; Giberto, 2008; see S2d).

In Argentina the pool of species was considered as the set of species sampled at least once in each locality/area. It is assumed that each species was distributed continuously between its northern and southern range boundaries, following models for estimates of diversity in littoral assemblages performed for the Western Atlantic and eastern Pacific coasts of North America (Roy et al., 1998, 2000) and in the Pacific coast of South America (Chile, Rivadeneira et al., 2002). According to Willig et al. (2003), dealing with the problem of a latitudinal gradient of decreasing richness from the tropical to the extratropical areas, there are several possible causes to explain this gradient, but in any case, the explanations are posterior to the discovery of the latitudinal gradient.

The material was obtained by means of bulk sampling (ca. 400 cc of matrix + biogenic content, atop shell concentrations to 30–50 cm deep). Selection of the fossiliferous deposits was determined on the basis of accessibility to the site, quality of preservation of the fossil molluscs and ages available from previous geochronological studies (S2a). All along the coast, the modern supralittoral and intertidal zones adjacent to the fossiliferous deposits were also sampled (ca. 400 cc bulk samples from each site) in order to provide modern records of benthic molluscan taxa living along the Argentine and Magellanean provinces, independently of the taxonomic lists available from traditional local catalogs. The sampling effort along the entire coast, fossil and modern, is considered sufficient to define patterns of regional diversity and environmental gradient.

The biotic composition, systematics and quantitative aspects of modern coastal settings from the SWA margin are still rather poorly or less well known compared to other littoral areas worldwide. There are still constraints regarding revised and updated taxonomic issues for different invertebrate groups (see Boltovskoy, 2007), especially for benthic bivalves and gastropods. In general, this applies to Argentina, Uruguay and Brazil, as well as northwards in South America to



**Fig. 2.** Synthesis of some physical features of the Mar Argentino within the SW Atlantic (SWA) according to studies available. Complete source of information, among others, in Parker et al. (1997), Piola and Rivas (1997), Acha et al. (2004), Giberto et al. (2004, 2007), Bogazzi et al. (2005), Romero et al. (2006), Boltovskoy (2007), Piola et al. (2010), references therein (S2). a. Synthesis of bottoms and currents. Substrate nature (modified from Parker et al., 1997). Shallow oceanic currents within the worldwide context and along Pacific and Atlantic South America; biogeographic provinces along the SW Atlantic (Malacological Provinces: An: Antillean; B: Brazilian; A: Argentinean; M: Magellanean). BC: Brazil Current; MC: Malvinas (Falkland) Current; PC: Patagonian Current; CZ: Subtropical–SubAntarctic Convergence Zone; CHC: Cabo de Hornos Current; HC: Humboldt Current; WWD: West Wind Drift (branch of the CAC); CAC: Circumpolar Antarctic Current (modified among others from Acha et al., 2004; Boltovskoy, 2007; Balech and Ehrlich, 2008). b. Sea surface temperature (SST), salinity, coastal zones, thermal and salinity fronts. Complete source of references in Boltovskoy (2007), Piola et al. (2008, 2010). Left: SST. Synthesized and modified from Acha et al. (2004). Right: Fronts. Synthesized and modified from Acha et al. (2004), Bogazzi et al. (2005). Numbers 1–3: Thermal fronts (1, Península Valdés Tidal Front; 2, North of Golfo San Jorge Front; 3, South of Golfo San Jorge Front). Letters A–D: Salinity Fronts (A, Río de La Plata Estuary Front; B, El Rincón Estuary Front; C, Argentine Shelf Break Front; D, Atlantic Patagonian Cold Estuarine Front). Subsurface Thermal Fronts (sensu Bogazzi et al., 2005): ERFS, El Rincón Frontal System; SMFS, San Matías Frontal System; NPFS, North Patagonian Frontal System; SPFS, South Patagonian Frontal System. Note that it has been well documented that the Río de La Plata plume exhibits a seasonal influence over the Bonaerensian, Uruguayan and Brazilian coasts (Piola et al., 2008, other references therein).

Surinam, Guyana, Venezuela. Consequently, qualitative estimations only are possible for those areas according to the present taxonomic information available. Further studies, considering new collections, updated systematic revisions, statistical analyses and sampling biases, will probably improve the patterns obtained. Regarding the Quaternary fossil assemblages, quantitative data are available only for selected sectors of the Argentine coastal area (references in Aguirre et al., 2008, 2009), therefore, only qualitative estimations are possible to establish regional comparisons.

Our database includes records for a total of 721 molluscan taxa (382 gastropods, 339 bivalves) from 57 age-period localities in 48 geographic areas: 29 Pleistocene sites, 28 Holocene and 35 from the modern littoral (Table 1; S1). Gastropods and bivalves were analyzed taking into account the fact that they represent the predominant biogenic content within the fossiliferous deposits and nearshore assemblages. Emphasis was placed on bivalves, due to their better preservation quality and higher palaeoecological value, and on the Holocene, due to the higher density and better geochronological control available for Argentina. A more complete source of information, including taxonomic composition, diversity (species richness and evenness), stratigraphic distribution, biogeographic ranges, life mode and habitat for each taxon, is available from more detailed studies performed in local areas and published elsewhere (S2b). Most data for Golfo San Matías (San Antonio Oeste surroundings-Puerto Lobos area) and southern Santa Cruz are as yet unpublished (Aguirre et al. unpublished).

#### 4.1. Dataset

Six dataset matrixes considering presence/absence records of gastropod and bivalve species were produced for Pleistocene, Holocene and modern sites. As a measure of biodiversity, one of the foundations of palaeoecological analyses, species richness (Hammer and Harper, 2006, p. 187) was calculated as the number of species present in each site per age-matrix. This simplest diversity estimation was chosen considering that quantitative data (relative abundance of taxa per sample, site, and time span) is not available for the entire geographic area analyzed or for all the age periods compared. Information on the relative abundance of each taxon in the samples, localities, areas and time span is only available for local selected sectors of Argentina and still need to be fulfilled for the northern Río Negro and southern Santa Cruz provinces (in course) while similar data for the remaining Atlantic South America are still missing.

**Table 1**  
Synthesis of the taxonomic groups considered by geographic areas and age periods.

	PL	HOL	MOD
Localities/areas			
SACA	3	3	5
BON	10	7	12
PAT	16	18	18
Total	29	28	35
Total molluscan taxa recorded: 721	95	140	721
Gastropod taxa (382)			
SACA	5	32	297
BON	20	46	117
PAT	39	43	76
Total	49	73	382
Bivalvia taxa (339)			
SACA	4	37	304
BON	24	51	91
PAT	28	30	46
Total	46	67	339

Emphasis was put on the bivalve results (due to their higher palaeoecological value and reliability in terms of post-mortem transport and taphonomic processes in the final depositional environment).

#### 4.2. Multivariate and cladistic analyses

Number of species was plotted against latitude; Cluster Analysis, Minimum Spanning Trees superimposed to Principal Coordinates Analysis and Parsimony Analysis of Endemicity (sensu Rosen, 1978) (PAE) were applied to all the matrices. An Area of endemism (AE) is here defined as an area of non-random congruent distribution of two or more taxa (sensu Morrone, 1994). Statistical analyses were conducted using the software Past version 2.02 (Hammer et al., 2001).

Cluster Analysis (CA) was performed calculating a similarity matrix (SM) using Jaccard index and using unweighted pair-group average (UPGMA) algorithm to obtain the fenogram. Upon the same SM calculated for CA, a Principal Coordinates Analysis (PCO) was performed together with a Minimum Spanning Tree (MST) superimposed to the tri-dimensional graphic representation of the PCO as a distortion measure.

PAE were performed with TNT version 1.1 (Goloboff et al., 2008) under maximum parsimony using equal and implied weights (Goloboff, 1993). Analyses with implied weighting were conducted by means of values for the concavity constant  $k=5-15$ . All tree searches were performed using a Wagner tree as starting tree and 1000 random addition sequences plus TBR with 100 trees to save per replication. The trees obtained then were swapped with TBR. The results obtained in this analysis were estimated as absolute and GC (Group present/Contradicted) frequencies with 1000 replicates of jackknife symmetrical resampling plus TBR, 10 random addition sequences, and saving 100 trees per replicate. Group support is used as argument to choose between the trees obtained from the different data sets and weighting regimes. To do this, the average support is calculated for each tree searches under the different weighting regimes.

The main results, illustrated and discussed beneath, first on diversity patterns and then on between areas relationships, emphasizing on Argentina and on bivalves, with some highlights on taxa which define areas of endemism, or are displaced at present or extinct in the SWA.

### 5. Results

Our results (Figs. 3 and 4) show the molluscan biodiversity at a regional scale, according to species range limits across the SW Atlantic, with emphasis in Argentina and in the marine Quaternary assemblages. A total of 151 taxa (78 gastropod and 73 bivalve taxa) were recorded in 29 Pleistocene sites (95 taxa: 49 gastropods, 46 bivalves) and 28 of Holocene age (140 taxa: 73 gastropods, 67 bivalves) (S1, S3; Table 1). Overall, a total of 116 taxa (48 gastropods, 68 bivalves) occur in the Quaternary of the Bonaerensian sector while 87 taxa (52 gastropods, 35 bivalves) occur in Patagonia. In the Bonaerensian area, the molluscan composition and distribution is as follows: 44 taxa in 10 Pleistocene sites (20 gastropods, 24 bivalves), 97 taxa in 7 Holocene sites (46 gastropods, 51 bivalves) and 208 in 12 modern sites (117 gastropods, 91 bivalves). In Patagonia, 67 taxa were recorded in 16 Pleistocene sites (39 gastropods, 28 bivalves), 73 taxa in 18 Holocene sites (43 gastropods, 30 bivalves) and 122 taxa in 18 modern sites (76 gastropods, 46 bivalves) (S4a, b).

As expected, a larger number of taxa were recorded in the modern littoral sites. Along most of the SW Atlantic a total of 721 taxa (382 gastropods, 339 bivalves) were recorded in 35 modern localities: 601 (297 gastropods, 304 bivalves) in Surinam, Brazil or Uruguay; in Argentina 208 taxa (117 gastropods, 91 bivalves) occur in the Bonaerensian area and 122 taxa (76 gastropods, 46 bivalves) in Patagonia (S4a, b).

5.1. Modern diversity patterns

The modern diversity results (Fig. 3a) show a large-scale geographic pattern based on site species richness for bivalves (mostly infaunal suspension feeders) and gastropods (mostly free epifaunal taxa), either separately or for both groups combined. Firstly, they exhibit a distinct latitudinal pattern, peaking in the North (tropical and subtropical localities at Surinam and Brazil) and decreasing southwards at higher latitudes (Patagonia). Secondly, within this regional pattern, a clearly low diversity can be observed for wide areas of the shelf characterized at present by lower salinity gradient, soft bottoms and higher turbidity. These lowest peaks (minimum values marked with down arrows in Fig. 3a) fit with sites characterized by local estuarine and marginal marine conditions, mostly influenced by freshwater discharge from the huge RLP through its seasonal plume (northwards in winter along the Uruguayan and Brazilian coast reaching ca. 28–27°S; in summer at the RLP outlet and southwards along the Bonaerensian coast reaching Mar del Plata surroundings) (Lucas et al., 2005; Piola et al., 2008).

Other areas are influenced by smaller rivers, creeks or coastal lagoons: in southern Brazil at Lagoa dos Patos and Lagoa Mirim surroundings, in the Uruguayan-Argentinian “delta” margin (outlet of the Paraná-RLP fluvial system), and smaller sectors of the Uruguayan and Bonaerensian littoral (e.g., Montevideo, Mar Chiquita, Las Brusquitas, Quequén Grande, Quequén Salado, Bahía San Blas) (Fig. 1, S1).

By contrast, the highest diversity values for Argentina correspond to the oceanic Bonaerensian coast adjacent to a neritic front. The highest peak is observed at Bahía Blanca surroundings, an area with a homogeneous water column down to 30 m deep, where a coastal front and thermal and salinity fronts have been recognized (Acha et al., 2004) (Fig. 2b); although periodically influenced by low salinity waters, it can be regarded as an area out of the strong influence of the Río de La Plata plume.

On the other hand, all along Patagonia the species richness trend is relatively uniform, but decreases slowly with latitude, reaching its minimum at Tierra del Fuego in the Patagonian cold estuarine zone/estuarine cold conditions (Acha et al., 2004; Bogazzi et al., 2005).

5.2. Diversity patterns through time

Diversity profiles obtained for the Holocene and Pleistocene datasets, for bivalves, gastropods and for the two groups combined, are in general terms very similar. The Holocene profiles for the bivalves (73 taxa) and the gastropods (67 taxa) are also similar to the modern trend. For the Pleistocene minor differences were observed between the bivalve (46 taxa) and gastropod (49 taxa) profiles. The Pleistocene bivalve pattern curve is more similar to the Holocene and modern pattern than is the Pleistocene gastropod pattern.

Emphasis was put on the bivalve results (due to their higher palaeoecological value and reliability in terms of post-mortem transport

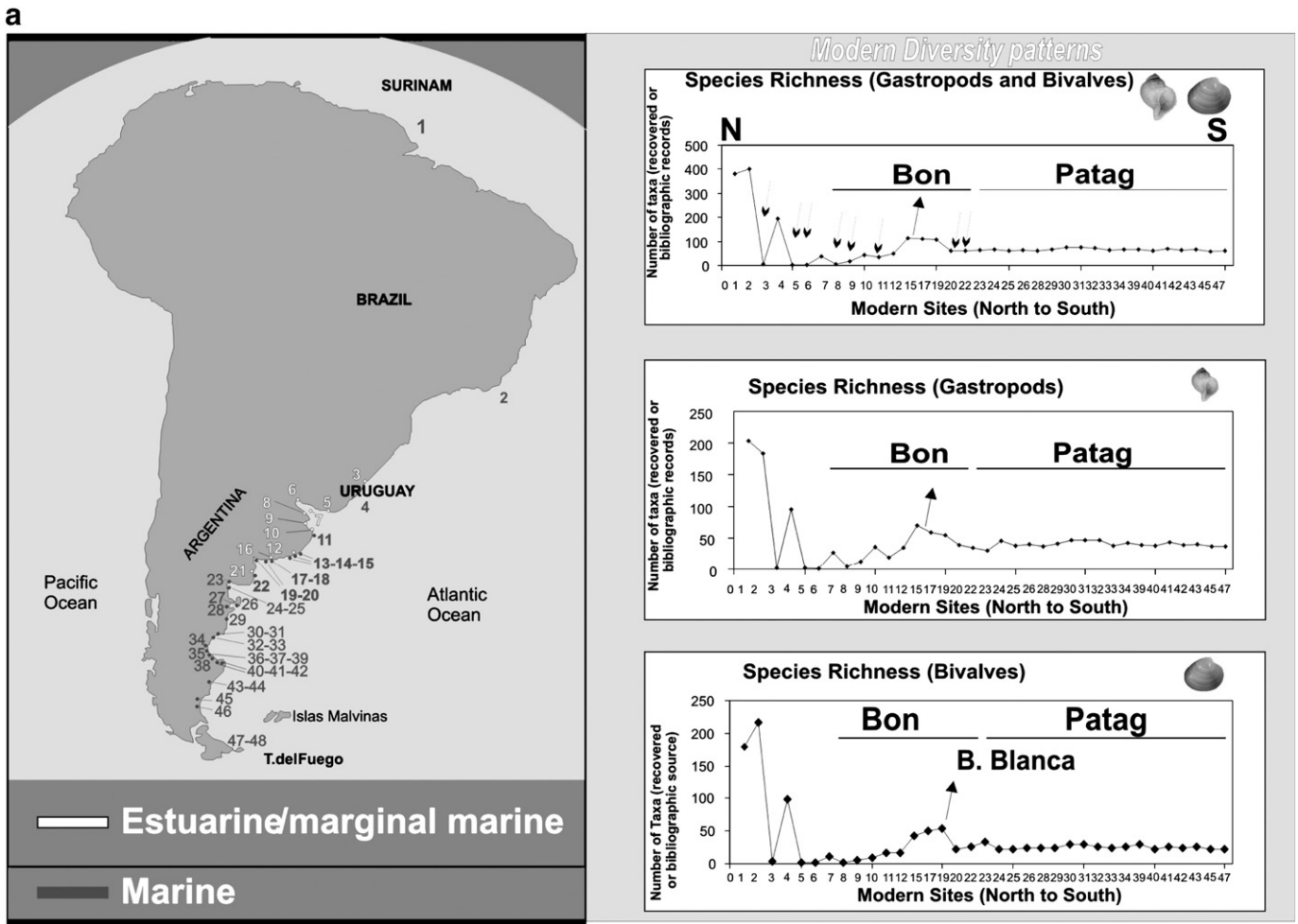


Fig. 3. Diversity patterns: modern and through time. a. Large scale modern diversity (species richness) patterns observed for bivalves, gastropods and for both groups combined. Numbers refer to the localities analyzed ordered latitudinally. N: north. S: south. Bon: Bonaerensian littoral. Patag: Patagonia. Bon and Patag are in Argentina. b. Comparative diversity patterns through time (modern, Holocene, Pleistocene) based on bivalves. Numbers refer to the localities analyzed (see S1) ordered latitudinally. N: north. S: south. Bon: Bonaerensian littoral. Bon and Patagonia are in Argentina.

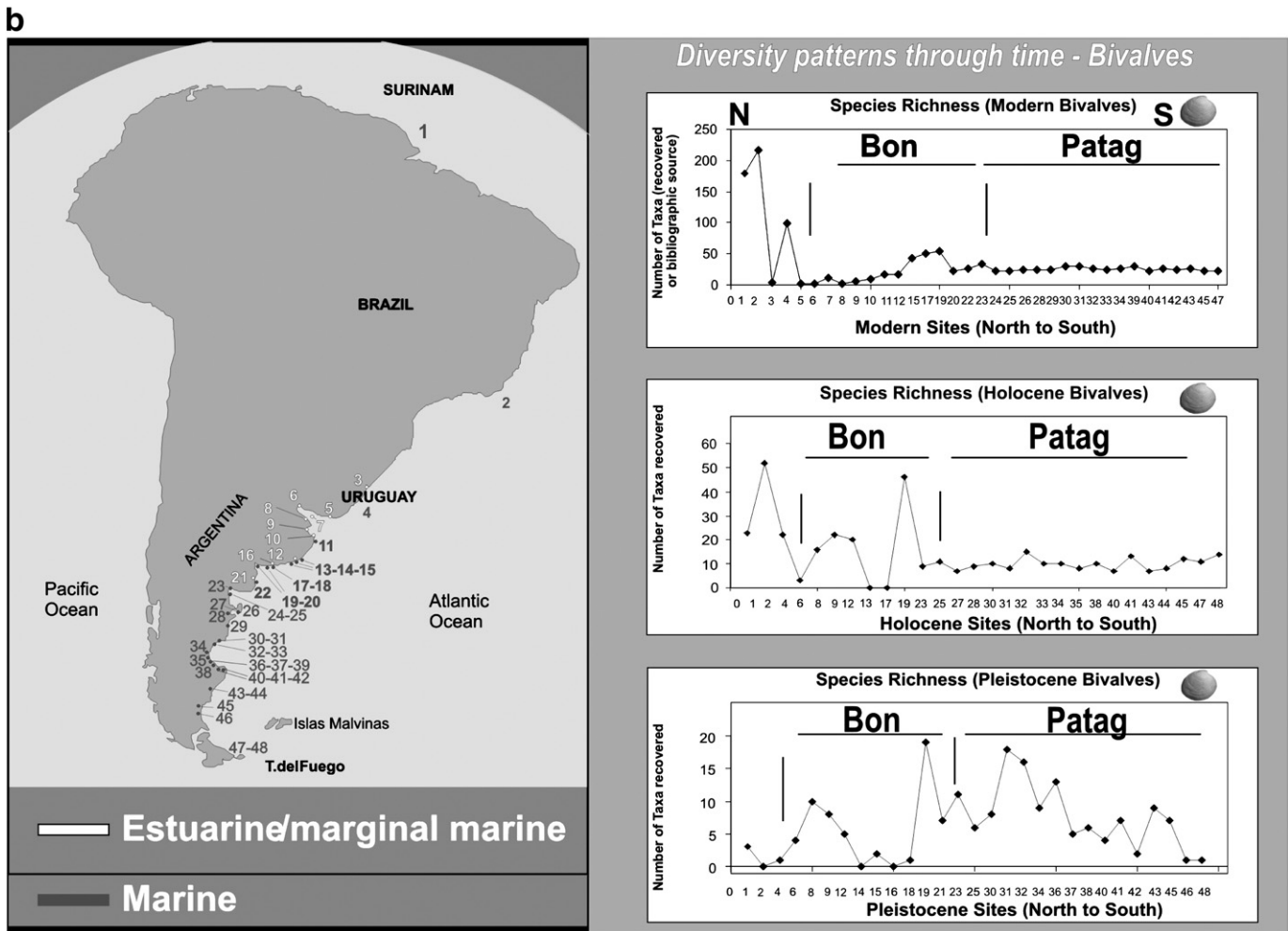


Fig. 3 (continued).

and taphonomic processes in the final depositional environment). Diversity patterns for bivalves through time (Fig. 3b) show that, especially for Argentina, the Holocene species richness curve is nearly identical to the modern pattern, peaking in the north and decreasing southwards, with the same minima coinciding with lower salinity palaeoenvironments (tidal flats and coastal lagoonal facies characterized by estuarine or euryhaline taxa; see S1).

The pattern observed for the Pleistocene deposits, is less complete and therefore more open to interpretation. These records include a time span with considerable bias in terms of time and geographic distribution, especially in the northern localities along the SW Atlantic, where they are scarcer or unknown, and in Patagonia where they are more abundant but in some cases of doubtful age. Despite these biases and uncertainties, a clear geographic (latitudinal) pattern can still be observed along Patagonia where the most continuous, better exposed and well preserved Pleistocene marine terraces with rich molluscan concentrations are found.

For Argentina, peaks in bivalve species richness through time are located on the oceanic Bonaerensian area in the north, reaching the maximum value always at Bahía Blanca.

### 5.3. Patterns between localities/between areas relationships

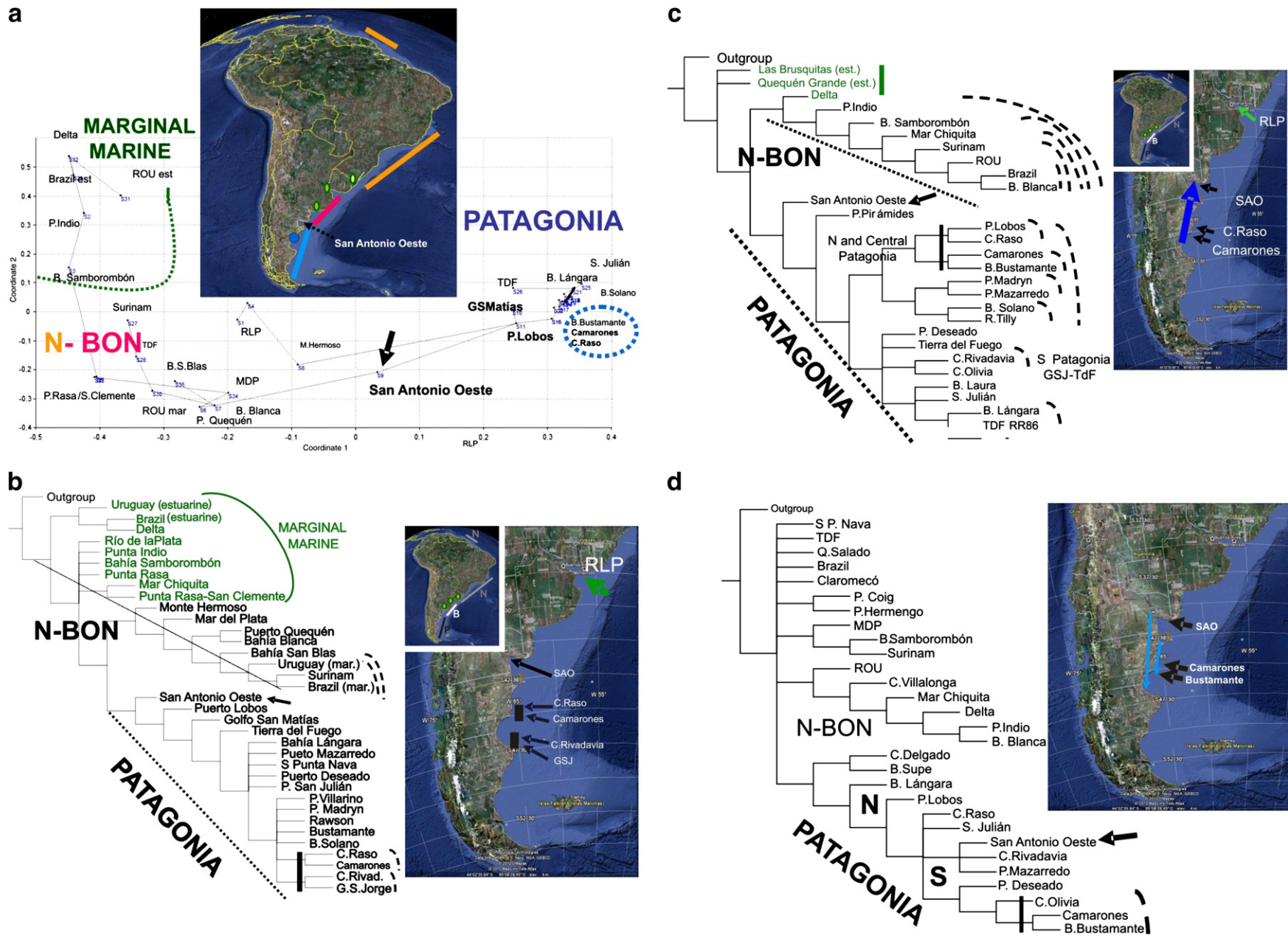
Independently of the approach used (CA, PCO, PAE), the relationships among the areas were in general terms congruent for the three age periods and taxa considered. Complete results for gastropods and bivalves, separately or combined, from different geographic areas and

ages, showed that bivalves, however, exhibited a clearer trend than gastropods. Only the bivalve results are synthesized in Fig. 4 using the PCO and PAE approaches.

For modern bivalves the three methods discriminate between marginal areas, oceanic northern South America-oceanic Bonaerensian localities (N-BON) and the Patagonian sites (Fig. 4). While CA (not shown) only allowed to discriminate between these three major groups of sites and coastal sectors, the PCO (Fig. 4a) is more useful to show the arrangement of geographic sites based on their taxonomic composition, showing the association or distance between localities more clearly. For example, in Patagonia, San Antonio Oeste (SAO) is apart from the remaining Patagonian sites and closer to GSM and Puerto Lobos (northernmost Patagonia), while Camarones-Bahía-Bustamante areas are more linked to central and southern Patagonian sites.

In turn, the PAE (Fig. 4b) was found to be the most useful tool for the recognition of natural patterns of organisms distribution (Crisci et al., 2003), confirming the same general groups but much better defined than the other methods (not shown). The application of this method clearly distinguished between separate marginal marine localities (e.g., estuarine Brazil and Uruguay, RLP, Punta Indio, Bahía Samborombón, Punta Rasa, Mar Chiquita), which could be considered a separate biogeographic unit along the SW Atlantic margin (a subprovince of the Argentine Malacological province?) and the oceanic N-BON area, more associated with marine sites from Patagonia. In the north, only Surinam–Brazil–Uruguay (ROU) was recognized as an area of endemism (AE) supported by six common shared taxa (*Noetia*





**Fig. 4.** Comparative between areas relationships. Patterns between localities based on bivalves: modern (a, b) and through time (c, d). ---: Areas of endemism (sensu Morrone, 1994). Localities shown in S1. a. PCO (Minimum Spanning Tree superimposed to Principal Coordinate Analysis); b. Parsimony Analysis of Endemicity (PAE). N: northern South America (Surinam, Brazil, Uruguay). BON: Bonaerian area. c. PAE for Holocene bivalves. d. PAE for Pleistocene bivalves.

*bisulcata*, *Pododesmus rudis*, *Crassostrea rhizophorae*, *Anomalocardia brasiliana*, *Petricola pholadiformis*, *Corbula caribaea*). In Patagonia, SAO lies apart, Cabo Raso-Camarones area appears more associated with central and southern Patagonia, where only two AE were recognized: Cabo Raso-Camarones (supported by four taxa; *Pitar rostratus*, *Eurhomalea exalbida*, *Protothaca antiqua*, *Clausinella gayi*), and C.Rivadavia-Golfo San Jorge (GSJ) (supported by three taxa; *Brachidontes purpuratus*, *Zygochlamys patagonicus*, *Pecten* spp.). Overall, the main site groups and subgroups of localities can be linked to latitude and to local environmental conditions: salinity, SST, substrate (Fig. 2). The PAE for the modern gastropods (not shown) evidenced the same pattern and allowed the recognition of the same AE, with more than fifteen taxa supporting the N-BON area and more than twelve taxa supporting Cabo Raso-Camarones-C.Rivadavia-GSJ as an AE. A few species can be mentioned whose range limits have implications for palaeoenvironmental interpretations: *Littoridina australis*, with its southernmost range endpoint in northern GSM, characteristic of the BON area; *Tegula patagonica*, with its southernmost limit at Puerto Deseado (although not recorded living between B. Bustamante and P. Deseado). It is important to note that *Tegula atra*, even when mentioned in the traditional bibliography as a typical modern Patagonian element and often illustrated in local catalogs as a common epifaunal gastropod species from the Atlantic Magellanean Province, has not been recorded in any of the modern samples collected or within the modern collections examined (see also Pastorino, 1991). Additionally, many specimens of this species examined from museum collections are not modern but, in fact, subfossil or fossil shells. We suspect that the Patagonian shells were collected from Quaternary marine terraces adjacent to the modern beaches and that they were washed along the modern shores.

The bivalve Holocene PAE (Fig. 4c) shows a pattern similar to that exhibited by modern bivalves (compare Fig. 4a vs. b). However, more AE were recognized in the Holocene than with the extant fauna. The spatial arrangement of the AE suggests that some molluscan taxa were probably southwards shifted in comparison with their present geographic ranges. The whole northern group of localities (N-BON; characterized by *Brachidontes rodriguezii*, *Tagelus plebeius*, *Macra isabelleana*) is more clearly defined in the Holocene and, at the same time, more homogeneous. Except for the estuarine Las Brusquitas and Quequén Grande localities which remain separate from the rest, altogether they represent an AE supported by several taxa (e.g., *Pitar rostratus*, *T. plebeius*, *Glycymeris longior*, *M. isabelleana*, *B. rodriguezii*, *Ostrea equestris*, *Nucula nucleus*, *Phlyctiderma semiaspera*) with four nested patterns (P. Indio, B. Samborombón, M. Chiquita, Surinam, ROU, Brazil, B. Blanca; note that Bahía Blanca is linked to Brazil). This more homogeneous pattern is an indication of more uniform and stable conditions in the Mid-Holocene than today especially regarding salinity and SST. In littoral areas where marginal marine conditions prevail at present, increased salinity conditions are expected to have occurred when they were covered by oceanic waters during the post-glacial transgression. Similarly, slightly higher SST are expected to have characterized the transgressive maximum during the Holocene Thermal Maximum; ca. 7–5 ka B.P.) as shown by taxa northwards displaced today (e.g., Aguirre, 1993a, b; Aguirre and Whatley, 1995).

On the other hand, the whole Patagonia is recognized as an AE during the Holocene, with two subgroups of localities, one in northern-central Patagonia (P.Lobos-R.Tilly/GSJ) and the other in southern Patagonia (P. Deseado) and Tierra del Fuego. In the first, the localities from Puerto Lobos to R. Tilly represent an AE with four nested smaller areas (P. Lobos-C.Raso; Camarones-Bustamante; P.Madryn-Mazarredo; B. Solano-R. Tilly) (*Protothaca antiqua*, *Clausinella gayi*, *Aulacomya atra*, *Aequipecten tehuelchus*, *Mytilus edulis*, *Brachidontes rodriguezii*). In southern Patagonia, only two AE were recovered: C.Rivadavia-C.Olivia (*Brachidontes purpuratus*, *A. atra*, *Eurhomalea exalbida*, *P. antiqua*, *C. gayi*), B.Lángara-T. del Fuego (*Mulinia edulis*, *E. exalbida*, *C. gayi*). Again, as in the modern bivalve PAE (Fig. 4b), SAO lies apart (San Matías Frontal System probably already active), but the C.Raso-Camarones-

Bustamante areas remain more linked to northern Patagonian sites (e.g., P. Lobos, northern GSM) than to central Patagonia (B.Solano, R.Tilly, GSJ), implying slightly higher Mid-Holocene SST. The Holocene gastropod PAE gave congruent results (not shown).

The Pleistocene bivalve PAE (Fig. 4d) shows a less clear pattern, especially for the northern area (N-BON), where more restricted fossiliferous deposits and less geochronological control also gave an unclear pattern of species richness. By contrast, the whole of Patagonia (characterized by the constant occurrence and dominance of *Protothaca antiqua* and abundance of *Eurhomalea exalbida*, *Clausinella gayi*, *Brachidontes purpuratus*, *Aulacomya atra*, *Ensis macha*), appears as a more clear, and rather homogeneous, area. The only AE, Camarones-B.Bustamante, is supported by more than ten common taxa among others *Diplodonta vilardeboana*, *Macra isabelleana*, *M. cf. patagonica*, *Venericardia procera*, *E. macha*, *Corbula patagonica* of which only a few (*M. isabelleana* and *M. cf. patagonica*, *D. vilardeboana* and *C. patagonica*) have northwards range endpoints at present. Curiously, SAO is more associated with southern Patagonia (G.S.Jorge-P.Deseado), implying generally lower SST compared to the Mid-Late Holocene and today. The Pleistocene gastropod PAE (not shown) gave a trend, in general terms, coincident with the bivalves and, for Patagonia, characterized by *Tegula atra*, in accordance with field observations performed for previous work published elsewhere (e.g., Aguirre, 2003; Aguirre et al., 2006, 2007, 2008, 2009; see other references in S2b).

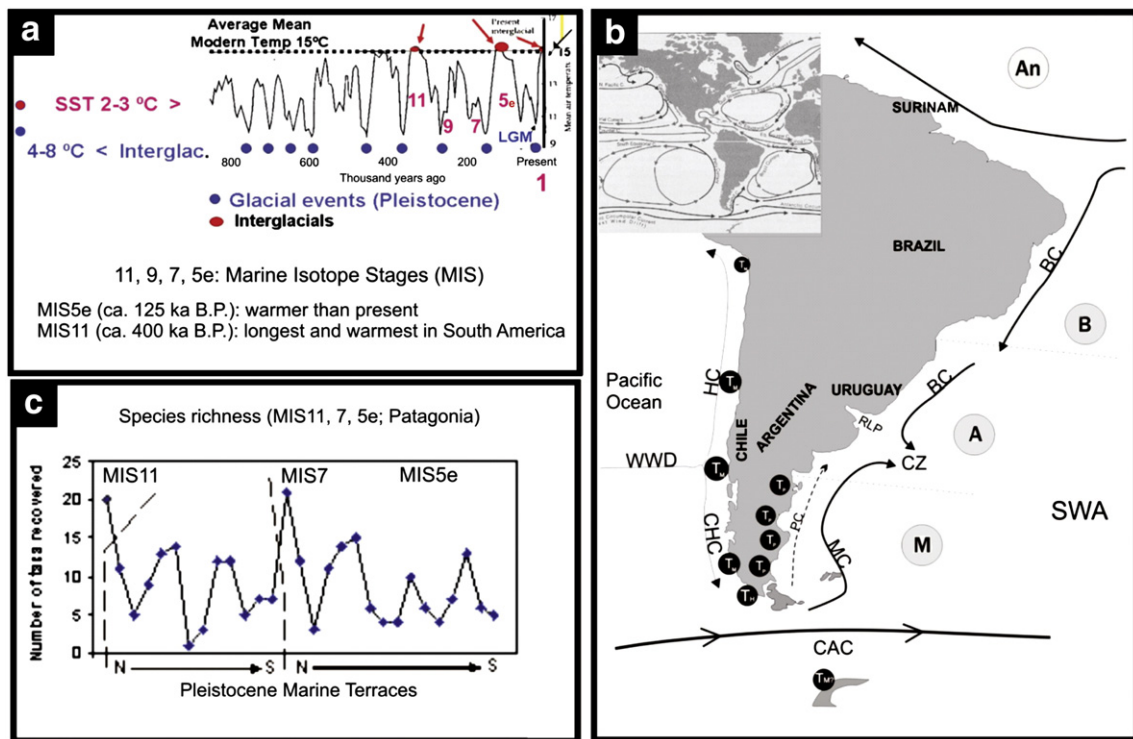
## 6. Discussion

### 6.1. Diversity patterns

The validity of a global latitudinal marine biodiversity trend has recently been called into question. Poleward declines along several areas of the Northern Hemisphere (mainly Pacific and Atlantic North America), asymmetry of trends between both hemispheres and between East and West, or dissimilar patterns within and among regions have been claimed for (e.g., Roy et al., 1994; Macpherson, 2002; Rivadeneira et al., 2002; Valdovinos et al., 2003; Jablonski et al., 2006; Valentine et al., 2008; Griffiths et al., 2009).

The modern species richness distribution shows a latitudinal large-scale regional biotic pattern. Our results for molluscs (bivalves and gastropods) show no apparent asymmetries between the NW (Roy et al., 1998, 2000, 2009) and SW Atlantic trends. Also, our molluscan evidence suggests that the modern SWA latitudinal trend is similar to that of the Mid-Holocene and pre-last glaciation levels (see similar evidence documented for the North Atlantic coastal plain since the Pliocene; Allmon et al., 1993). The Holocene and Pleistocene diversity trends are not remarkably different, especially along Argentina and in Patagonia, thus Pleistocene glacial-interglacial fluctuations seem not to have had dramatic effects (major extinctions?) on the benthic molluscan species richness as a whole. Probably, this is linked to more stable conditions of the nearshore waters, with smaller differences in SST between maxima highstands and glacial episodes compared with air temperature differences for terrestrial environments during the same episodes (Fig. 5a). There is abundant evidence of coastal marine faunas of the Last Interglacial (MIS5e), having survived the lower sea levels of the late Pleistocene (particularly MIS2), returning to the modern coast with the post glacial marine transgression with little change in the assemblages. For example, in the Southern Hemisphere, as in southern Australia, some changes in the molluscan fauna occurred from the Last Interglacial to the present (Murray-Wallace et al., 2000; J. Cann, pers. comm.), but in the main the faunas are extremely similar.

Several causal hypotheses (Roy et al., 1998, 2000; Rivadeneira et al., 2011; but see Gaylord and Gaines, 2000) have been postulated to explain latitudinal diversity patterns, for example, among others: 1) Rapoport's (1982) rule (geographic gradient as a result of decrease



**Fig. 5.** Schematic synthesis of the Quaternary littoral (marine) climatic scenario in Argentina. a. Reconstruction of sea-level, glacial maxima and average atmospheric temperature. Modified from Lomolino et al. (2005). LGM: Last Glacial Maximum. Quaternary interglacials preserved in Patagonia since ca. 400 ka B.P. are: MIS11 (ca. 400 ka), 9 (ca. 325 ka), 7 (ca. 225 ka), 5e (ca. 125 ka) and MIS1 (Mid-Holocene). The arrows indicate sea-level episodes higher than the present (Haq et al., 1987). According to the global isotope curve only two of the last Pleistocene interglacials could have been warmer than today (MIS11, MIS5e). Circles indicate maximum glacial events. On the left, average sea surface temperature (SST) differences between glacial maxima and interglacial highstands; average air temperature variations between glacial maxima and interglacial conditions. b. Pleistocene molluscan diversity along Patagonia. Species richness is more informative when discriminating between different MIS (not so informative when considered as a whole, see also Fig. 3b). Higher peaks belong to MIS11 and MIS5e, congruent with warm taxa northwards displaced today (e.g., *Chama* spp.; MIS5) or extinct (e.g., *O. tehuelcha*, MIS11). Only localities with our own quantitative records have been considered. Geochronological control of the deposits according to Rostami et al. (2000) Schellmann (2007), other references therein (S2). c. Schematic synthesis of the distribution of *Teguia atra* (Lesson) in South America. T<sub>M</sub>: modern records; T<sub>P</sub>: Pleistocene records; T<sub>H</sub>: Holocene records. Malacological provinces as in Fig. 2a.

in species range lengths towards the tropics); 2) species-energy (the pattern responds to total or average amount of available energy as function of solar radiation at the surface); 3) species-area effect (higher marine diversity in larger size shelf areas); 4) historical events (which in our Quaternary tectonically stable scenario could be represented by cyclic climatic fluctuations leading to habitat fragmentation); 5) the recent “out of the deep south” hypothesis (claiming for a combination of high latitude origin for taxa with deep bathymetry, taxonomic conservatism restricting dispersal of taxa towards lower latitudes, and higher speciation rates towards higher latitudes probably enhanced by disappearing glaciers after the Last Glacial Maximum; Rivadeneira et al., 2011; Kiel and Nielsen, 2010).

Firstly, results from our area are highly in accord with the species-energy hypothesis, assuming solar energy as a function of latitude and SST as a complex function of climate, ocean circulation and related parameters (Roy et al., 2000). In fact, mean SST and other associated parameters can account for much of the observed latitudinal variation in diversity along the SW Atlantic. The comparative across-time analysis of diversity for the coastal area of Argentina, showing similar latitudinal trends, peaking in the north and tailing off southwards, since the Pleistocene to the present (Fig. 3b), can be interpreted as a biotic response to SST, at least since ca. MIS11. This trend correlates, firstly, with solar energy input (average SST) and is probably linked to some aspect of primary productivity and trophodynamics, as diversity can be influenced by seasonal stability of trophic resources (e.g., Rex et al., 2005).

Coastal environments, once established, can remain relatively unchanged. Although it is widely known that in many coastal envi-

ronments worldwide, coastal processes are dynamic and rapid evolution of coastal landforms following culmination of the postglacial marine transgression are well documented (e.g., Codignotto et al., 1992; Cann et al., 1999, 2009). Most probably, changes in coastal environments lead to changes in the molluscan faunas.

Secondly, at local scales, salinity and substrate nature may have had a control over the type, number and relative abundance of individual taxa present at different geographic areas and time spans. For instance, the highest modern species richness in Argentina (Fig. 3a; M.del Plata, P. Quequén, B.Blanca) matches with sites of the oceanic Bonaerensian littoral characterized by sandy substrates, out of the influence of the RLP, whereas the maximum peak at B.Blanca coincides with a very homogeneous shallow water column, in a zone of thermal and salinity fronts (Acha et al., 2004; Fig. 2b). Conversely, lowest peaks for South America and Argentina (estuarine Brazilian sites like Lag. dos Patos and marginal marine Uruguayan sites; in Argentina: the delta margin, RLP, B. Samborombón, M. Chiquita, M.Hermoso, B. San Blas) concur with zones with fine substrates (mostly muddy bottoms) characterized by waters of high organic matter content and turbidity, mainly under the seasonal influence of the RLP plume (Piola et al., 2008) or, southwards, out of the RLP influence, within El Rincón Estuarine Frontal System (Bogazzi et al., 2005) (Fig. 2a, b). This is supported by studies by Lucas et al. (2005) showing that between 34 and 43°S three major basins (RLP, El Rincón and G.San Matías) are influenced by three large river discharge effects (Paraná-RLP, R.Colorado and R.Negro). On the other hand, the more homogeneous part of our modern littoral species richness profile corresponds to varied substrate types along Patagonia, in agreement with more uniform salinity conditions along an entirely oceanic littoral, which is influenced by the Malvinas cold, salty, nutrient-rich waters and,

closer to the coastline, by the lower-salinity cold Patagonian current. Also, between 37 and 50°S in the Argentine Sea, a shelf-break front determines a vertical mixture of water column upwelling in cold oxygenated waters of high productivity (Acha et al., 2004). At SAO, the slightly higher diversity is probably due to a higher salinity gradient (via higher evaporation) and SST (via circulation reversals) in the area of the San Matías Frontal System (Piola and Rivas, 1997; Bogazzi et al., 2005; Lucas et al., 2005).

For the Pleistocene, independently of the general similar diversity trend (Fig. 3b), species richness is much more informative when discriminating between different highstands (MIS). This is only possible to analyze along Patagonia, where very well preserved marine terraces were assigned to MIS11, 9, 7, and 5. According to the global isotope curve (Fig. 5a), only two Pleistocene high sea-level episodes were warmer than today: MIS11 (ca. 400 ka B.P., the longest and warmest in South America; Ortlieb et al., 1996a, b) and MIS5e (Last Interglacial maximum, ca. 125 ka B.P.). In accordance with this, the highest species richness obtained for the Patagonian Pleistocene sites coincide with marine terraces assigned to MIS5e and 11 (San Antonio Oeste; Camarones-Bahía Bustamante area) (Fig. 5b). Moreover, warm species northwards displaced at present (e.g., *Chama* spp.) have been recorded within MIS5e at SAO (see also Pastorino, 1991), while some northwards displaced or extinct taxa (*Macra* cf. *patagonica*, *Diplodonta vilardeboana*, *Corbula patagonia*, *Macoma uruguayensis*, *Aequipecten tehuelchus*, *Ostrea tehuelcha*) characterize MIS11 at Camarones area (see also Aguirre et al., 2006, 2007). In summary, these are independent sources of evidence showing that molluscan diversity in our area is linked to SST.

Our results support other similar trends based on different sources of evidence from the SWA. For example, studies based on modern species richness of marine bryozoans in the continental shelf of Argentina (Lopez Gappa, 2000), with higher diversity northwards and in shelf areas dominated by coarse sediments along a high productivity shelf-break front. Also, a highest number of planktonic species was documented in the subtropics rather than in transitional, subpolar or polar water masses of the SW Atlantic (Bolotovskoy, 1982). In general terms, they are also in agreement with evidence for the Atlantic Ocean from 80°N to 70°S (Macpherson, 2002) based on fishes and invertebrate groups (pelagic and benthic habitats).

Another point to be made is that our results agree with molluscan research showing that a latitudinal marine diversity pattern is valid for infaunal (most of our bivalves) as well as for epifaunal molluscan taxa (our gastropods) which is not in accord with Thorson's (1952) hypothesis assuming that such a trend applies to marine epifaunal taxa only. The fact that the same diversity trend is observed for bivalves and gastropods, represented by predominant infaunal suspension or deposit-feeders and by free epifaunal elements, respectively, and is repeated for the modern, Holocene and Pleistocene datasets, is evidence that the trends are not a product of sampling bias or incomplete fossil database.

On the other hand, our geographic diversity pattern does not match with the latitudinal asymmetric trend (highest diversity at higher latitudes) documented for the eastern Pacific along southern South America as suggested by different marine taxa (e.g., Rivadeneira et al., 2011: "out of the deep south" hypothesis). Furthermore, our results do not seem to be directly linked to any species-area control on diversity as suggested for the Chilean margin (higher species richness southwards linked to wider continental shelf area; Rivadeneira et al., 2002; Valdovinos et al., 2003). In contrast to this, the Argentine continental shelf is more expanded southwards and the lowest diversity values match with the widest sector of the Argentine continental shelf.

According to the information available, diversity asymmetries in the Southern Hemisphere (SH) seem to characterize only the southeastern Pacific margin, along the cold estuarine fjords of the southern Chilean coast. The highest species richness reported at southern latitudes was

interpreted to be a result of the higher oxygen levels available and of hypothesized Quaternary glacial refugia during the last glaciations (Rivadeneira et al., 2011). They could also be interpreted to have resulted, however, from relatively uniform, constantly cold and low salinity waters during the whole Quaternary fluctuations to the present, enhancing diversity. During the last ca. 800 ka, the Pleistocene climatic cycles, separated by ca. 100 ka, must have caused average air temperature variations of ca. 4 and 8 °C between glacial–interglacial maxima (Fig. 5a), most probably implying very rapid and dramatic changes for terrestrial biotic responses. By contrast, in terms of marine benthic biotas, minor variations of mean SST between glacial–interglacial episodes (up to ca. 2–3 °C) likely resulted in less dramatic changes in the marine environment, with more stable conditions leading to more homogeneous habitats and diversity patterns. Alternatively, local variations in ocean circulation could have affected the timing and quantity of nutrient availability (Roy et al., 1998). In the SWA Pleistocene, marine refugia seem so far undocumented, perhaps due to relative stability of niche availability, including trophic resources. Asymmetric diversity trends or Pleistocene marine refugia seem not to be a general rule for the SH.

In a worldwide context, in comparison with other areas of the SH as South Africa, Tasmania, New Zealand, Antarctica and subantarctic islands (Kerguelen, Crozet, Prince Edwards, Bouvet), the South American regions showed similar or smaller numbers of species, far lower than in the Indian Ocean or in the Western Pacific (Troncoso et al., 2001; Linse et al., 2006; Griffiths et al., 2009).

Moreover, in the Southern Ocean no sign of an East–West diversity disparity was found (Mollusca, Pycnogonida), perhaps a consequence of the marked homogeneity effect of the West Wind Drift and relatively uniform water temperature and general physical conditions, with very few barriers to dispersal (Griffiths et al., 2009). Based on the greatest similarity for several taxonomic groups (Bryozoa, Pycnogonida, Bivalvia) the Subantarctic islands were considered more influenced by South America than by New Zealand or Australian signatures. Even past connectivity between different regions of Antarctica (e.g. transantarctic seaways connecting the Weddel Sea with the Ross Sea shelves) could be a response to the Western Antarctic Ice Sheet collapse ca. 1.1 Ma B.P. (Barnes and Hillenbrand, 2010; Bryozoa), thus an Antarctic origin (Weddell Sea?; Linse et al., 2006), at least for certain molluscan taxa present in the Quaternary and modern littoral in southern South America, cannot be ruled out.

## 6.2. Areas of endemism and patterns between localities

Interpretations of patterns between localities through time (Fig. 4) suggest that the last cyclic climatic fluctuations had effects (not dramatic) on the benthic littoral molluscs (bivalves and gastropods), although slightly noticeably when examined at narrow local geographic scales or individual sites. The biotic responses are expressed by northwards or southwards shifts of groups of sites defined through PCO combined with AE recognized through PAE. Geographic areas of maximal species turnovers are generally assumed to represent the boundaries for biogeographic units and are located at boundaries between major water masses. In the Mar Argentino our molluscan evidence document that they probably changed accompanying global SST changes and subsequent high and low sea-level episodes as during MIS2.

Considering that among the most important physical factors which control the composition and distribution of benthic littoral molluscan associations, substrate, SST and salinity determine their geographic ranges and boundaries for modern biogeographic units, changes in patterns between localities during the Pleistocene and mid-Holocene could respond mainly to the same controls. Precisely, these patterns show that Patagonia has always been a relatively homogeneous area; C. Raso-Camarones-B.Bustamante represents an AE since the Mid-

Pleistocene, the only uniform, distinct AE through time, suggesting similar substrate nature and salinity.

In the modern PAE (Fig. 4b), the entire locality groups are linked to latitude and to local physical factors, e.g. SAO, apart from the rest of the Patagonian sites, exhibits local conditions: fine bottoms (sands and clays), higher salinity (more evaporation) and higher SST (maximum time of residence of the water in the internal area), within an area of salinity and thermal fronts in the so-called San Matías Frontal System (Guerrero and Piola, 1997; Acha et al., 2004; Bogazzi et al., 2005). Warmer waters at SAO (Fig. 2b) allow the occurrence of taxa which are absent southwards, determining a species turnover starting southwards of this locality. Interestingly, both the PCO and PAE techniques have been powerful and useful to show this clearly (Fig. 4a, b). Besides, the best supported AE in N-BON area belongs to oceanic coastal settings of higher salinity and SST (Surinam, southern Brazil and Uruguay). Moreover, in Patagonia, the AE defined by Cabo Raso-Camarones and C.Rivadavia-Golfo San Jorge match with surrounding areas where surface thermal fronts were recognized, the so-called Tidal North Patagonian Frontal System and the South Patagonian Frontal System, respectively (Fig. 2b). Recent studies showed that the distribution of life at the spatial scale in the Mar Argentino is strongly linked to frontal spatial patterns and marine fronts as key factors controlling feeding and reproductive strategies and migratory patterns of local populations (Acha et al., 2004; Bogazzi et al., 2005; Romero et al., 2006).

For the Mid-Holocene and Pleistocene, the PAE results reveal shifts in spatial patterns for sites and AE and show key species (e.g., *Chama* spp., *Tegula atra*) which decipher that climate changes influenced the littoral biota, probably through alterations of the atmospheric-oceanic circulation patterns and runoff configurations, which are the main controlling factors at present (e.g., Guerrero and Piola, 1997; Piola and Rivas, 1997; Palma et al., 2004).

The more homogeneous Mid-Holocene PAE pattern, where the N-BON area can be recognized as a large AE, suggests more uniform and higher salinity gradients at various zones where marginal marine conditions prevail at present. Such conditions could be a consequence of marine waters influencing the coastal area during the Mid-Holocene transgressive maximum when the coastline was a few km westwards relative to its modern position, even when the marine transgression was minor and it is likely that the eastern coast of South America was subject to the effects of hydroisostasy. On the other hand, this pattern implies slightly higher SST (ca. 2 °C in comparison with the modern pattern for the Mar Argentino; Hoffmann et al., 1997; Acha et al., 2004) and a southern shift (ca. 400–500 km?) of the water masses in coincidence with the so-called Thermal Maximum (Kaufman et al., 2004; Briner et al., 2006) documented ca. 7–5 ka B.P. Along the Bonaerensian sector, a probable biotic response to this maximum allowed the occurrence of several taxa northwards displaced today (e.g., *Triphora nigrocincta*, *Anachis avara*, *Urosalpinx rushi* among the gastropods; *Noetia bisulcata*, *Anomalocardia brasiliana*, *Petricola pholadiformis*, *Crassostrea rhyzophorae*, among the bivalves). Independently, a southwards decrease in relative abundances of warm and warm-temperate molluscan taxa during the Mid-Holocene (highest in coastal landforms older than 5–4.5 ka B.P.) and increase of cold taxa (highest in deposits younger than 4 ka B.P.) southwards to ca. 45–47°S (Aguirre et al., 2009, references therein) support that interpretation. A southern shift during the Mid-Holocene of the South Atlantic Anticyclonic center, the Brazilian current and the shallow water masses, could have caused displaced endpoint boundaries for the geographic ranges of stenothermal warm-temperate taxa. For the Bonaerensian area this is supported by isotope data (Aguirre et al., 1998, 2002). In addition, the Holocene PAE shows that SAO still remains apart from the rest of the Patagonian localities, confirming a similar circulation pattern to the modern one in this area (salinity and thermal fronts). But C.Raso-Camarones-Bustamante, more linked to the northern sites (e.g., P. Lobos in GSM) than to central Patagonian sites, suggests slightly higher SST conditions. Independently,

this is supported by higher relative abundance of taxa living today in subtropical-temperate waters of the Argentine province (*Glycymeris longior*, *Amiantis purpuratus*, *Pitar rostratus*, *Buccinanops* spp., *Olivancillaria* spp.). Probably, the 2–3 °C SST increase postulated worldwide during the Mid-Holocene (Kaufman et al., 2004; Briner et al., 2006) may not have had a remarkable impact on the number of species, but on the relative abundance and/or geographic ranges of stenothermal taxa which were southwards shifted ca. 5–7 ka B.P. (Aguirre, 1993b; Aguirre and Farinati, 1999; Aguirre et al., 2008, 2009) compared to their modern southern endpoints. The Holocene general trend, based on our collection records, agrees only partially with previous bibliographic compilations (e.g., Gordillo, 1998), probably due to different taxonomic criteria and/or to the fact that in our study the materials collected have been analyzed separately according to their age along the Bonaerensian or Patagonian sectors.

In the Pleistocene PAE, in Patagonia the fact that SAO is southwards shifted and linked to southern sites (P. Mazarredo, P. Deseado) implies that the modern thermal front seen at this place was not active or not as important at that time. The southern shift of Camarones-B. Bustamante area, linked to C.Olivia in a well supported AE, also suggests a predominant colder coastal scenario as a whole, probably through a more intensified, stronger, cold Malvinas current. Some thermally anomalous molluscs provide an independent source of evidence, for example, the dominance of *Tegula atra* within marine Pleistocene terraces from Patagonia (especially within MIS9, MIS7 and MIS5 south of San Antonio Oeste), in huge quantities and with maximum size shells, associated with abundant large shells of cold *Fissurella* spp. or *Mulinia edulis*.

*Tegula atra* is a cold water gastropod living only in the eastern Pacific coasts of Chile up to southern Peru (Fig. 5c). At present *T. atra* is extinct in the SW Atlantic, with no records in the Holocene from Argentina. In Chile it has Holocene records in the Magallanes region (Cárdenas and Gordillo, 2009) (and probably in the Pliocene, Nielsen, oral com. 2010). A doubtful modern record was reported for Antarctica (Linse, 1999). Changes in the oceanic circulation pattern after the Last Glacial Maximum (LGM) could be a reason for its extinction in the SW Atlantic. Based on its stratigraphic and geographic patterns, *T. atra* can be regarded as a biostratigraphic indicator species for the Pleistocene (Aguirre et al., 2009) and as a palaeoceanographic indicator species. Probably it colonized the SW Atlantic during the Late Neogene from the south, from the Pacific or from SubAntarctic islands or Antarctica, dominating during the Pleistocene in predominantly colder SST. But it probably became extinct after the LGM with the Holocene amelioration and consequent greater influence of the Brazil current or less intensified Malvinas current (an indication of palaeoceanographic changes after the LGM?). Curiously, *T. atra* is absent in Pleistocene (MIS5e) deposits from SAO, where abundant *Chama* spp. (northwards displaced at present; see for example Pastorino, 1991) suggest higher SST than present, in agreement with the highest diversity peak and with warmer conditions suggested by the global isotope curve. Moreover, the dominance of *T. atra* in the Pleistocene implies that, even during warm Pleistocene interglacial episodes the Patagonian littoral was characterized by a general cold climatic scenario south of SAO, which has ever since represented a species turnover area for molluscs, and that its extinction is most probably linked to changes in palaeoceanographic conditions in the SW Atlantic after the LGM (winds, direction and intensification of marine currents, oxygen and nutrient availability, dispersal pathways).

## 7. Concluding remarks

The Late Quaternary nearshore molluscan fossil assemblages from Argentina are not identical to the modern molluscan associations. They show (minor) differences either in taxonomic composition or in their spatial patterns. They suffered changes to present (quantitative,

geographic displacements, a few extinctions), providing palaeoenvironmental, palaeoclimatic and, in some cases, palaeoceanographic information.

Latitudinal salinity barriers along the SWA (e.g., Lag. dos Patos, Río de La Plata, El Rincón Estuarine system, Golfo San Matías), temperature gradients (through winds, oceanic currents, water masses) and hydrodynamic forces (RLP plume, San Antonio Oeste reversal, intensity of Brazil and Malvinas shallow currents) explain the modern distribution of species richness and between areas relationships. Molluscan variations since the Mid-Late Pleistocene represent a biotic response to differences in some of those parameters linked to sea-level and climatic changes.

In summary, regarding diversity:

- A modern latitudinal species richness cline decreasing towards the southern pole applies for bivalves (mostly infaunal taxa) and gastropods (mostly epifaunal taxa), from Surinam to Tierra del Fuego. This trend is linked primarily to SST, secondarily to salinity. The highest peaks fit with fully marine coastal sectors in warmer waters (thermal and salinity fronts), minimum peaks with local estuarine or marginal marine conditions.
  - No asymmetry between the SWA and NW Atlantic (e.g., Jablonski et al., 2000) modern latitudinal species richness trends are apparent.
  - Along the Mar Argentino the molluscan evidence does not require hypotheses of Quaternary refugia or mosaic of niches for survivors of Pleistocene glaciations to explain the diversity and spatial patterns observed and some Antarctic species could have colonized this area from the south, even during pre-Quaternary times.
  - Overall, this trend did not change dramatically through time but seems rather similar to the Mid-Holocene (MIS1) and pre LGM (Mid-Late Pleistocene) patterns, in agreement with Neogene marine evidence from the North Atlantic coastal plain (e.g., Allmon et al., 1993).
  - In Patagonia, species richness discriminated between several well preserved Pleistocene highstands showed highest peaks during MIS11 and MIS5e, together with taxa northwards displaced at present or extinct (e.g., *Maetra cf. patagonica*, *Diplodonta vilardeboana*, *Corbula patagonia*, *Macoma uruguayensis*, *Aequipecten tehuelchus*, *Ostrea tehuelcha*, *Chama* spp.), suggesting episodes of warmer SST in agreement with the global isotope curve.
- Regarding patterns between localities, multivariate (CA, PCO) and cladistic (PAE) methods have been useful to test explanations of large scale palaeobiological patterns between modern, Mid-Holocene and Pleistocene assemblages. Overall, these approaches provided similar results, discriminating between estuarine and marginal marine from open marine sites. PCO combined with PAE was most advantageous for our study area, allowing more objective, clear, quick comparisons based on an abundant database.
- We have recognized AE which varied through time. Mid-Holocene and Pleistocene shifts in the spatial relationships between localities and of the AE are a result of minor changes in salinity, SST and circulation.
  - During the Mid-Holocene a more homogeneous littoral environmental and climatic scenario is assumed in the SWA. Higher salinity gradients characterized sites which today are influenced by the huge Río de la Plata plume and show estuarine/marginal marine conditions. A slightly higher (ca. 2 °C) SST than today influenced the Bonaerensian and north-central Patagonian coastal sectors, probably during a Thermal Maximum (7–5 ka B.P.), allowing an intensified Brazilian current and warm water masses facilitating southwards shifts of some bivalve and gastropod taxa. SAO thermal and salinity fronts (San Matías Frontal System) may have been already active.
  - During the Pleistocene in Patagonia, even within slightly warmer interglacials (e.g., MIS5e), south of SAO the nearshore seems to

have been characterized by a colder climatic scenario, testified by dominance of *Tegula atra* together with other cold water taxa (e.g., *Fissurella* spp., *Mulinia edulis*). The thermal front seen today at SAO may have been then not as active or as important.

- *T. atra* (absent today in the SWA, abundantly preserved in the Patagonian Pleistocene within MIS9, 7, 5e) is a useful biostratigraphic and palaeoclimatic indicator species, probably a signal of post-LGM palaeoceanographic changes (higher intensity of the cold Malvinas current previous to the Holocene amelioration).

In conclusion, between areas relationships, are an artifact of the SW Atlantic geography and historical events: local and temporal changes in SST, salinity, thermal and salinity fronts, RLP plume extension, oceanic circulation patterns. Our patterns through time are explained in terms of salinity fluctuations while marine waters covered extensive coastal areas during transgressive phases, especially via coastal estuaries and lagoons. Also, even a ca. 2–3 °C rise in SST during high sea-level episodes probably enhanced dispersal of larvae of certain taxa and greater nutrient availability with proliferation of higher diversity levels, geographic shifts and changes in relative abundances of individual taxa. Our results and inferences are consistent with and complement previous studies providing evidence of local geographic compositional or quantitative variations of some dominant taxa in response to Mid-Late Quaternary climatic cycles (Aguirre et al., 2009; other references in S2b).

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