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Quaternary Marine Mollusk Associations of the Last Interglacials in North Patagonia (Argentina): Paleoecology and Paleoclimates

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Abstract

Deposits of different Quaternary marine transgressions are largely exposed in the Argentine north Patagonian littoral (39°15'S–41°02'S), south of the Buenos Aires and north of Río Negro provinces. The malacological associations of 84 sites were studied. Among them, 31 belong to Pleistocene deposits of the interglacials $\geq$ MIS 9, MIS 7, MIS 5e, 29 to Holocene deposits of the interglacial MIS 1, and 24 sites of modern beaches. These sites yielded 7385 fossils among valves and shells, of 78 species (42 bivalves and 36 gastropods), including 11 micromolluskan species. The record of the bivalves *Crassostrea rhizophorae* in the south of the Buenos Aires Province, and *Anomalocardia brasiliiana* (both currently inhabiting lower latitudes), and very likely the gastropod *Tegula atra* (inhabiting today the Pacific Ocean) in the north of Río Negro Province, suggests that interglacials MIS 7, MIS 5e and MIS 1 were warmer than today. However, the associations determined for the studied interglacials have not changed in their composition, but in abundance of species, except for the latitudinal shifts of the three mentioned species, and the presence of cold to temperate water taxa since the MIS 1 in the ecotonal area of the north of Río Negro Province. Changes in the associations of northern Patagonia during the Quaternary derived from global changes (sea surface temperature, salinity, etc.), and the existence of habitat heterogeneity in each of the areas, that enabled the co-existence of different bivalve and gastropod species of the local benthic marine malacofauna.

Keywords: quaternary, mollusks, paleoenvironments, paleoecology, north Patagonia

1. Introduction

1.1 Quaternary in the world

The Quaternary is characterized worldwide by important climate oscillations, with extremes represented by glacial and interglacial periods resulting from temperature variations that caused marked changes in sea level (e.g., [1]). In coastal areas, transgressive-regressive events have generated a sequence of erosion forms (coastal terraces and paleocliffs) and beach deposits that, for different reasons, have

been protected from degradation processes and are therefore an important testimony of climate changes that have occurred in most recent geologic time [2].

1.2 Glacial and interglacial cycles

In 1941, Milankovitch developed a planetary theory that attributes Quaternary glacial and interglacial cycles to modifications of orbital parameters such as eccentricity (100 Ka), obliquity (41Ka), and precession of the equinoxes (19 Ka).

Since the beginning of the Pleistocene, climatic oscillations would have followed periodic cycles of about 40 Ky that seem to conform the variation cycle of the earth axis. The amplitude of the cycles tended to increase 1.5 My ago, and from 600 Ka the glacial cycles have occurred at intervals of between 80 and 120 Ky (e.g., [3, 4]). This duration of the recent cycles is similar to the period of variation of the eccentricity of the earth orbit, of 100 Ky.

1.3 Marine isotopic stages (MIS)

The different glacial and interglacial events occurred during the Quaternary were differentiated through the marine isotope stages (MIS). These MIS represent alternate cold and warm periods established on the basis of $\delta^{18}O$ of benthic foraminifers, obtained from cores of the sea bottom [5]. Emiliani [6] divided the last million years in successive isotopic stages on the basis of the $\delta^{18}O/\delta^{16}O$ relationship. Each isotopic stage represents a glacial period (designated with an odd number) or interglacial (designated with an even number), and reveal the advance and retreat of the ice during the last glaciations.

1.3.1 Interglacials in the world

Globally, the MIS 11 encompasses from 424 to 374 ka. It was a long warm period that reached a global mean sea level of 6 to 13 m above the present one between 410 and 400 ka [2]. Some authors (e.g., [7–9]) consider the MIS 11 as an analogous of the Holocene both in climatic conditions and orbital forcing. According to Ashton et al. [10] the climatic conditions in marine isotopic and ice sheet records include at least two large warm episodes with an intermediate cooling phase. The warm conditions of this interglacial were reflected in different marine and terrestrial communities (e.g., [9, 11, 12]).

MIS 9 encompasses from ca. 330 up to 310 ka and sea level was 3 ± 3 m below the present one [13]. In the Northern Hemisphere, at Henderson Island ($24^{\circ}22'S/128^{\circ}20'W$), the highest sea level recorded in MIS 9 is between 334 ± 4 and 324 ± 3 ka in agreement with the maximum sun insolation of 333 ka [14]. In the western Mediterranean (Spain) the sea surface temperature (SST) and the salinity recorded in this interglacial were similar to those of MIS 7 and MIS 5e [15], whereas other authors (e.g., [16]) suggested that according to paleontological evidence, this interglacial was warmer than MIS 7 and the Holocene, and similar to MIS 5e.

MIS 7 encompasses from ca. 245 up to 190 ka [17] with three temperature maximums [18]. Isotopic data of some deep sea cores suggest that the sea level would not have reached the level of the present one [19, 20], although other authors suggest values around -18 m [17]. SST of this interglacial was higher than the present one [21–23]. In the European coasts, the marine deposits of MIS 7 record the appearance of the “Senegalese” marine fauna from the African coast, confirming this stage as warm in the Northern Hemisphere (e.g., [24–26]). Similar conditions are observed in the Southern Hemisphere: the SST of the southern Argentine Patagonia (42° – $43^{\circ}S$) is proposed to be similar or slightly warmer than today on the basis of the record of warm water mollusks (e.g., [27, 28]).

MIS 5 in the substage e, is one of the most studied episodes, and best represented worldwide. It encompasses from ca. 130 ± 2 to 119 ± 2 ka [29] and the SST was

approximately 2°C higher than the present one (e.g., [30, 31]). Comparing with other interglacials, MIS 5e has the best records of SST [18]. Evidence of warm water benthic mollusks, and changes in their geographic distribution was found in MIS 5e (e.g., [5, 26, 27, 32–48]).

MIS 1 encompasses the last 11.7 ka [49], when the last glaciation is considered to be ended [50]. There is an increase of the SST and humidity worldwide (e.g., [4, 51–56]) with some records in the Southern Hemisphere (e.g., [37, 49, 50, 57–59]). This phenomenon is reflected worldwide in the biotic communities with changes in composition, abundance, diversity and distribution (e.g., [60–62]).

In the Argentine Patagonian region, the stages MIS 11 to MIS 1 are represented, as well as ingressions older than MIS 11, but with poor records and fossil content [32].

2. Area of study

2.1 Quaternary marine deposits from the northern Argentine Patagonia

Along the Argentine coast, broad extensions of the littoral of the Buenos Aires Province (BAP) and north Patagonia were affected by accumulation and erosion processes produced by sea level oscillations during Quaternary transgressions (e.g., [63, 64]).

Northern Patagonia has been divided into two regions according to their province. The first groups three areas of the south of the BAP (A-C) and record the presence of the interglacials $\geq$ MIS 9, MIS 5e and MIS 1 [5, 65, 66], and the other one belongs to region D, and records the presence of the interglacials $\geq$ MIS 9, MIS 7, MIS 5e, and MIS 1 (**Figure 1**).

In region A, from Peninsula Verde to Otero Island, the transgressive deposits have been assigned to the Sangamon (? Late Pleistocene), which are represented in the area of the Colorado River delta by paleocliffs associated with coast lines up to 10 m height [67]. These marine deposits are assigned to the oldest interglacials because of their geomorphological, altimetric and cementation similarity [68]. Among them, there are scarce, thin, and isolated deposits on the continent which are assigned to $\geq$ MIS 9 [68, 69].

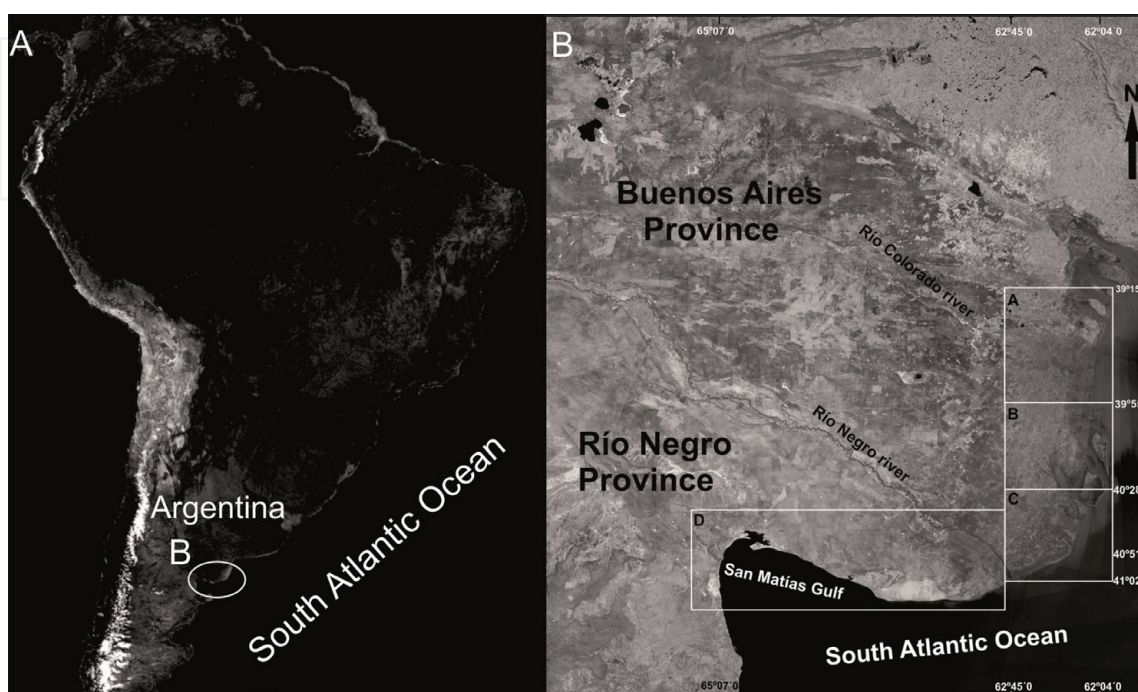


Figure 1.
(A) Map of study, and (B) four areas in the northern Patagonia in Argentina.

The terminal area of the delta is formed by the marine deposits of the MIS 1 ingress, which are beach ridges or intertidal environments [68].

In region B, which extends from the Otero Island to near the Jabalí Island, Weiler [70] correlated the Pleistocene and Holocene marine deposits of the central area with three transgressive events of the Late Pleistocene and Holocene, and related them to environments of barriers and coastal lagoons of the transgression of the Sangamon interglacial (with a minimum age of 43 Ka), the interstadial transgression of the middle Wisconsin (38.5 to 25 Ka), and the postglacial transgression of the MIS 1 (middle Holocene, between 5 and 5.2 Ka). More recently, Schnack et al. [71] related the oldest deposits of the area described by Weiler [43] with the Interglacial MIS 5e, considering the radiocarbon datings as minimum ages.

In region C, from the Jabalí Island up to Villa 7 de Marzo, Fucks et al. [68] reinterpreted the stratigraphic sequences, assigning a minimum of four transgressive cycles. Beach ridges, as well as beach strand plains and tidal plains, with maximum altitudes of 6 m a.s.l. and very clear morphologies are present from the coast to the present day continent, particularly in Isla Jabalí. Above them, at altitudes of 8 to 10 m a.s.l. that increase gradually to over 30 m a.s.l., clear ridges could be probably related to MIS 5e. These could have been originated in two ≥ 9 transgressive events.

In region D, north of San Matías Gulf from near the El Cóndor beach up to Las Grutas beach, there are records of the interglacials MIS 7, MIS 5e and MIS 1 plus a fourth one, 60 m height, that probably corresponds to an interglacial $\geq$ MIS 9. According to Fucks et al. [72] the deposits of interglacials MIS 7 and MIS 5e correspond to Baliza San Matias and San Antonio formations, respectively, and those of Holocene age have no designation.

The main geomorphological features are littoral ridges formed by high energy conditions, although, deposits corresponding to intertidal environments, coastal lagoons, spit sand cliffs forms have been described mainly for the Holocene transgressive event as well (e.g., [5, 68, 72–75]).

All these deposits contain marine mollusks, particularly gastropods and bivalves (Figure 2) (Table 1) [5, 35–37, 65, 82].

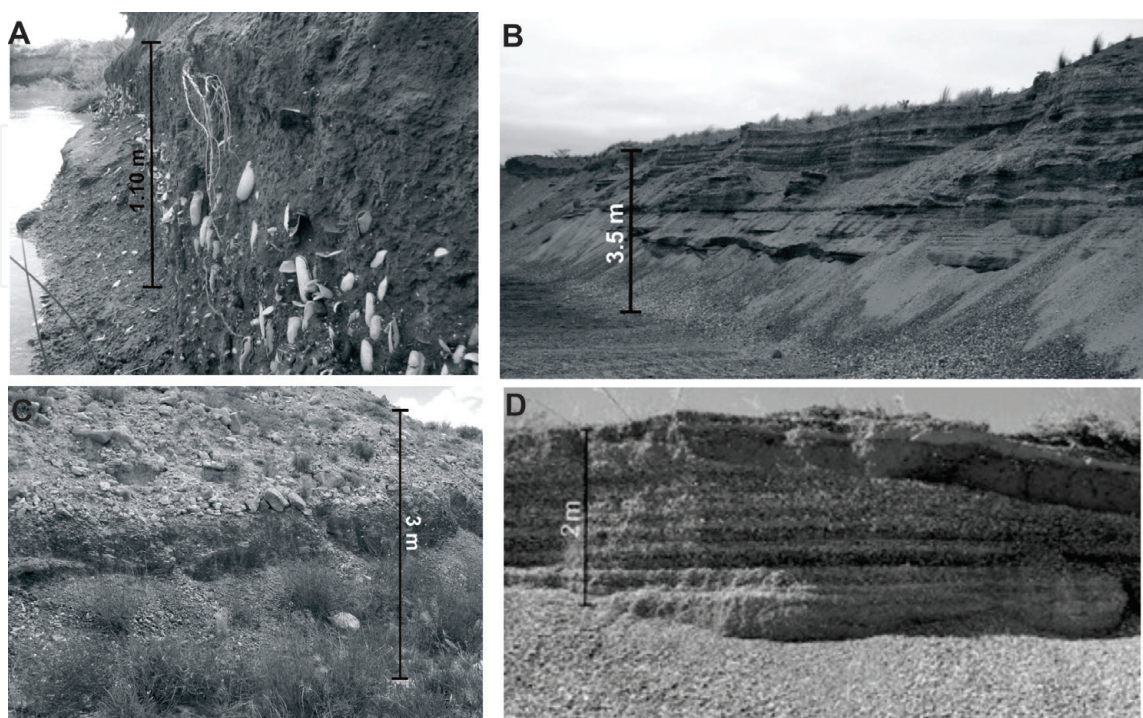


Figure 2.

(A) Profile of Holocene deposit with *Tagelus plebeius* in life position (region a, MIS 1); (B) Holocene littoral ridge in canal Villalonga (region B, MIS 1); (C) Pleistocene outcrops near Cardenal Cagliero locality (region C, MIS 9) and (D) Holocene cliff near San Antonio Este Harbor (region D, MIS 1).

Province	Área	Coordinates (Lat-long)	Sites	Ages (14C and ESR)	Altitude (m.a.m.s.l)	Cites
South of Buenos Aires	Delta del río Colorado	39°20'S;62°04'W–39°55'S;62°08'W	P. Verde (39°21'S;62°5.9'W)	2170 ± 86 ka	5–2.5	[76]
			Pta Laberinto – río Colorado Viejo (39°30'S–39°50'S)	6.63 ± 0.12 ka–0.409 ± 0.10 ka	10–7.5 and 2	[74]
			Sur del río Colorado viejo (39°53'S; 62°10'W)	9.46 ± 0.12 ka–0.407 ± 0.10 ka	5–2.5	[74]
	Bahía Anegada	39°55'S;62°08'W–40°28'S;62°11'W	Pleistocene deposits (40°03'S–40°26'S)	43 ka, 38.55 ka, 25 ka	40–25	[70, 77]
				43 ka, 38.8 ka, 31 ka	10–7	[75]
			Canal Villalonga (40°1'S; 62°19'W)	5.98 ± 0.10 ka–3.69 ± 0.10 ka	4–2.5	
	Isla Jabalí – Villa 7 de marzo	40°36'S;62°11'W–41°1'S;62°45'W	Los Pocitos (42°25'S; 62°25'W)	4.4 ± 0.08 and 4.5 ± 0.09 ka	3	[72, 74, 78]
			Oeste de isla Jabalí (40°40'S;62°30'W)	30.78 ± 1.65 ka–28.4 ± 0.80 ka	3–9.5	[75, 79]
			Isla Jabalí (40°34'S;62°13'W)	5. 37 ± 0.11 ka–2.17 ± 0.11	4–5	[37]
			Faro Segunda Barranca (40°46'S;62°16'W)	102–108 ka 94.5, 79 and 72.7 ka 28 a 40 ka	8–10	[80, 81]
Northern of Rio Negro	Norte del golfo San Matías	40°51'S;65°7'W–41°02'S; 62°49'W	Caleta Falsa correlation with localities: south of Piedras Coloradas	≥230 and ≥169 ka	8–12	[80, 81]
			Baliza San Matias (40°42'S; 64°51'W)	97.3–83 ka	8	[73]
			La Rinconada (40°41'S;65°9'W)	107–91 ka	10	
			Las Grutas (40°48'S;65°4'W)	70.3–66.8 ka	10	
			La Conchilla (40°49'S/64°52'O)	2.43 ± 0.60 ka	1.50	[5]

Table 1.
Absolute dating available from the study área.

3. Materials and methods

3.1 Methodology for marine mollusks associated with littoral deposits

A total of 84 localities were studied in two areas, 31 Pleistocene, 29 Holocene, and 24 modern ones. In these localities 7385 valves and shells of mollusks were collected. Each coastal deposit to be studied is identified on topographic maps. At each level of the site, a volumetric sample of 1 dm³. In contrast, at modern beach sites the sample is taken in a quadrant 1 m x 1 m along transects perpendicular to the coast line.

Each fraction of biogenic content recovered from the sieves (2.80, 1.40 and 0.080 mm) was identified, measured with digital caliper, and labeled. Species were identified through catalogs and specific literature.

Valves and shells found in the marine deposits are considered as assemblages representing the accumulation of non-contemporary individuals in a single set, and occurs because the time of generation of these individuals is faster than the burial rates. In this context, it has to be taken into account the changes produced during the transition of the animal remains from the biosphere to the lithosphere, which is studied through a discipline called taphonomy (etymologically derived from the Greek taphos, tomb, and nom, law). Taphonomy was defined by Efremov [83] as the science that studies the laws of burial, and accepted that taphonomic processes lead to the loss of information and are the cause of gaps in the fossil record. Currently this concept has been reversed since numerous studies (e.g., [84–87]) support the idea that the faunal associations of both current and fossil valves provide relevant information on living communities, or paleocommunities, being able in both cases to reconstruct the environments or paleoenvironments from the analysis of the faunal associations and thus interpret environmental and climatic changes.

The studied mollusks form transported faunal associations, which, according to different authors, preserve compositional fidelity concerning taxonomy and relative abundance of the communities that inhabited each environment within the considered period, and represent the accumulations of non-contemporary individuals as a whole.

4. Results

4.1 Marine malacology of northern Patagonia

The four areas identified in northern Patagonian according to their geomorphology (A-D), in which 84 sites were studied, yielded 78 species (42 bivalves and 36 gastropods). Eleven of them are micromollusks: *Heleobia australis*, *Olivella tehuelcha*, *Parvanachis isabellei*, *Turbonilla argentina*, *Turbonilla paralaminata*, *Chrysallida multituberculata* (gastropods) and *Nucula nucleus*, *Ennucula grayi*, *Carditamera plata*, *Corbula patagonica*, and *Corbula lyoni* (bivalves) (**Tables 2 and 3**).

4.2 Malacological analysis

Seventy species were identified in areas A-C (37 bivalves and 33 gastropods), and 45 species in region D (19 bivalves and 24 gastropods), with a similarity of 51.3% in bivalve species and 48.5% in gastropods.

In areas A-C, all the studied sites assigned to the interglacial $\geq$ MIS 9, are paleobeaches and littoral ridges; i.e., high energy environments in which the marine fauna is euryhaline (salinity > 30–35 gr/l) and of sandy substrate. Warm water species prevailed in bivalve associations (50–67%) compared to the other interglacials recorded in the area. However, no bivalve or gastropod of warm lineage that constitutes itself a paleoindicator was found.

Bivalves	Salinity	Life habit	Depth (m)	Substrate	Trophic type	Distribution area
<i>Nucula (N.) nucleus</i> [88]	E	I	0–200	S	D	23°S–53.5°S
<i>Ennucula grayi</i> (d’Orbigny, 1846) ¹	E	I	5–1850	S	D	22.93°S–55.5°S
<i>Adrana electa</i> [89]	E	I	20–75	S	D	22.93°S–39°S*
<i>Glycymeris (G.) longior</i> [90]	E	I	10–75	S	Sf	10°S–42°S
<i>Mytilus edulis platensis</i> (d’Orbigny, 1846) ¹	P–E	Ep	0–50	H	Sf	68°N–55.5°S
<i>Brachidontes (B.) rodriguezii</i> (d’Orbigny, 1846) ¹	P–E	Ep	0–25	H	Sf	34°S–42°S
<i>Aulacomya atra</i> [91]	E	Ep	0–30	H	Sf	34°S–55.5°S
<i>Aequipecten tehuelchus</i> (d’Orbigny, 1842) ¹	E	Ep	10–120	M	Sf	21°S–42.58°S
<i>Atrina seminuda</i> [92]	P–E	Ce	0–3	H	Sf	35°N–35°S*
<i>Plicatula gibbosa</i> [93]	E	Ce	0–120	H	Sf	35.3°N–34°S*
<i>Ostreola equestris</i> [94]	P–E	Ce	0–80	H	C	37°N–42°S
<i>Ostrea puelchana</i> (d’Orbigny, 1841) ¹	P–E	Ce	0–70	H	C	22°S–42°S
<i>Crassostrea rhizophorae</i> [95]	P–E	Ce	0–50	H	C	21.4°S–35°S
<i>Crassostrea gigas</i> [96]	E	Ce	0–40	H	Sf	Cosmopolitan
<i>Diplodonta (D.) patagonica</i> (d’Orbigny, 1842) ¹	E	I	36–102	S	Sf	21°S–42.58°S
<i>Diplodonta (F.) vilardeboana</i> (d’Orbigny, 1846) ¹	E	I	25–77	S	Sf	21°S–42°S
<i>Carditamera plata</i> [97]	E	I	17–70	S	Sf	23°S–39°S*
<i>Trachycardium muricatum</i> [88]	E	I	0–11	S	Sf	35°N–42°S
<i>Mactra guidoi</i> [98]	P–E	I	0–25	S	Sf	34°S–42°S
<i>Mactra isabelleana</i> (d’Orbigny, 1846) ¹	P–E	I	0–25	S	Sf	23°S–42°S
<i>Raeta (R.) plicatella</i> [99]	P–E	I	0–11	S	Sf	39°N–41°S
<i>Mesodesma mactroides</i> [100]	E	I	0–20	S	Sf	23°S–41°S
<i>Solen tehuelchus</i> [101]	E	I	10–18	S	Sf	23°S–39°S*
<i>Macoma (P.) uruguayensis</i> [102]	E	I	18–70	S	D	29°S–39°S*
<i>Angulus gibber</i> [97]	E	I	13–55	S	D	23°S–43°S
<i>Abra (A.) aequalis</i> [94] ¹	E	I	0–50	S	D	35°N–23°S*
<i>Tagelus (T.) plebeius</i> [103]	P	I	0–10	S	Sf	42°N–54°S
<i>Tivela isabelleana</i> (d’Orbigny, 1846) ¹	E	I	0–55	S	Sf	21°S–42°S
<i>Anomalocardia brasiliiana</i> [104]	P–E	I	0.3–5	S	Sf	18°N–39°S*
<i>Pitar (P.) rostratus</i> (Philippi, 1844) ¹	E	I	10–100	S	Sf	22°S–38.7°S*
<i>Amiantis purpurata</i> (Dillwyn, 1817) ¹	E	I	0–20	S	Sf	19°S–43°S
<i>Retrotapes exalbidus</i> [105]	E	I	50–70	S	Sf	34°S–55.5°S

Bivalves	Salinity	Life habit	Depth (m)	Substrate	Trophic type	Distribution area
<i>Ameghinomya antiqua</i> [106]	E	I	5–50	S	Sf	34°S–54°S
<i>Panopea abbreviata</i> (Valenciennes, 1839) ¹	E	I	25–75	S	Sf	23°S–48°S
<i>Corbula</i> (C.) <i>patagonica</i> (d’Orbigny, 1846) ¹	E	I	15–90	S	Sf	23°S–43°S
<i>Corbula</i> (C.) <i>lyoni</i> [107]	E	I	11–67	S	Sf	19°S–43°S
<i>Cyrtopleura</i> (S.) <i>lanceolata</i> (d’Orbigny, 1846) ¹	E	I	10–27	S	Sf	6°S–42°S
<i>Barnea lamellosa</i> (d’Orbigny, 1846) ¹	E	I	15–150	R	Sf	34°S–43°S
<i>Lyonsia</i> (L.) <i>alvarezii</i> (d’Orbigny, 1846) ¹	E	I	50–86	S	Sf	38.3°S–41°S
<i>Periploma ovatum</i> (d’Orbigny, 1846) ¹	E	I	?	S	Sf	35°S–40.5°S
<i>Thracia similis</i> [108]	E	I	50–86	S	Sf	22°S–42.58°S

Ep, epifaunal; *I*, infaunal; *Ce*, cemented; *H*, hard; *S*, soft; *C*, carnivorous; *D*, detritivorous; *He*, herbivore; *Sf*, suspension feeder; *O*, oligohaline (3–8‰); *M*, mesohaline (8–18‰); *P*, polyhaline (18–30‰); *E*, euhaline (>30–35‰).

¹Taxa found in the studied area.

¹The references of species are found on MolluscanBase eds (2021).

Table 2.
Ecological requeriments and distribution of bivalves.

Interglacial MIS 5e is represented in all the studied sites mostly by littoral ridges in which most associations are euryhaline, of sandy substrate and subordinate rocky substrate. Most species are epifaunal except in region A, prevailing filter feeders and carnivores. The proportion of warm water species in this interglacial is lower than in the previous one (44–50%) being outstanding the record of the warm lineage bivalve *Crassostrea rhizophorae*, excellent paleoindicator. In region D, this proportion is only 27% of the bivalves.

Interglacial MIS 1 was recorded in the whole study area, with two types of deposits in areas A-C: littoral ridges (high energy environments) and tidal plains (low energy environments). In the first ones, the malacofaunal associations are mostly euryhaline, of sandy substrates. In the second ones instead, the associations vary in salinity from oligohaline to mesohaline-polyhaline (salinity between 3 and 30 gr/l), of fine sand substrate, mostly epifaunal and filter feeders prevailing infaunal and carnivores in region A. This latter would be related to the modern geomorphological features of low energy environments (wide tidal plains, tidal channels and non-functional fluvial courses), that resulted in the formation of islands which can be seen in all the southern coast of the Buenos Aires Province. This interglacial MIS 1 is recognized in area D in littoral ridges, being the malacofaunal associations mostly euryhaline, of sandy substrate with rocky subordinate. In the associations of MIS 1 there is 45 to 50% of warm water species in areas A-C, unlike areas D in which this proportion is only 18% of the total bivalves.

In modern beaches of the south of BAP, but not in the northern sector of Bahía Anegada there are sandy beaches together with mud-sandy ones, and malacofaunal associations correspond to marine parameters of high energy, euryhaline of sandy substrate with scattered rocky substrate, mainly in area C. Instead, the modern

Gastropods	Salinity	Life habit	Depth (m)	Substrate	Trophic type	Distribution area
<i>Nacella (P.) magallanica</i> [104]	E	Ep	0–200	H	He	38.5°S–55.5°S
<i>Diodora (D.) patagonica</i> (d’Orbigny, 1841) ¹	E	Ep	0–15	H	He	11°N–45°S
<i>Fissurella radiosa radiosa</i> (Lesson, 1831) ¹	E	Ep	0	H	He	48°S–55°S
<i>Lucapinella henseli</i> [109]	E	Ep	0–55	H	He	23°S–
<i>Calliostoma carcellesi</i> (Clench and Aguacho, 1940) ¹	E	Ep	0–60	S	He	40.37°S–41.67°S
<i>Calliostoma coppingeri</i> [110]	E	Ep	13–86	S	He	30°S–44.21°S
<i>Tegula (A.) patagonica</i> (d’Orbigny, 1835) ¹	E	Ep	0–57	H	He	23°S–54°S
<i>Tegula atra</i> (Lesson, 1830) ¹	E	Ep	0–9	H	He	38°S–55°S
<i>Bostrycapulus odites</i> [111]	E	Ep	0–46	H	Sf	25°S–45.8°S
<i>Crepidula argentina</i> [112]	E	Ep	30–50	H	Sf	38°S–41.03°S
<i>Crepidula dilatata</i> [113]	E	Ep	0–66	H	Sf	35°S–55.8°S
<i>Notocochlis isabelleana</i> (d’Orbigny, 1840) ¹	E	I	0–113	S	C	22.4°S–42.58°S
<i>Heleobia australis</i> (d’Orbigny, 1835) ¹	O, P, M	Ep	0–60	M	He	24°S–41°S
<i>Epitonium (E.) georgettinum</i> (Kiener, 1838) ¹	E	Ep	0–101	M	He	23.37°S–44.27°S
<i>Epitenium striatellum</i> (Nyst, 1871) ¹	E	Ep	30	M	He	23°S–41°S
<i>Trophon patagonicus</i> (d’Orbigny, 1839) ¹	E	Ep	0–50	H	C	32°S–40°S
<i>Trophon geversianus</i> [114]	E	Ep	0–58	H	C	36.42°S–54.98°S
<i>Urosalpinx cala</i> [107]	E	Ep	28–28	H	C	32°S–41°S
<i>Zidona dufresnei</i> [115]	E	Ep	10–90	S	C	23°S–42°S
<i>Adelomelon (P.) brasiliana</i> [116]	E	Ep	0–250	S	C	23°S–52°S
<i>Adelomelon beckii</i> [117]	E	Ep	40–75	S	C	20° S–52°S
<i>Odontocymbiola magallanica</i> [104]	E	Ep	10–200	M	C	35°S–55.2°S
<i>Marginela martini</i> (Petit, 1853) ¹	E	Ep	10–80	S	C	22.93°S–42°S
<i>Olivella (O.) tehuelcha</i> [118]	E	Ep	15–57	S	C	23.69°S–43°S
<i>Olivancillaria urceus</i> (Röding, 1798) ¹	E	Ep	5–50	S	C	19°S–42°S
<i>Olivancillaria carcellesi</i> [119]	E	Ep	0–22	S	C	23°S–42.5°S
<i>Olivancillaria uretai</i> [119]	E	Ep	0–30	S	C	23°S–40.6°S
<i>Buccinanops monilifer</i> [120]	E	Ep	0–50	S	C	35°N–42°S

Gastropods	Salinity	Life habit	Depth (m)	Substrate	Trophic type	Distribution area
<i>Buccinanops cochlidium</i> [105]	E	Ep	5–66	S	C	23°S–42.58°S
<i>Buccinanops globulosus</i> [120]	E	Ep	0–6	S	C	35°S–46°S
<i>Buccinanops uruguayensis</i> [107]	E	Ep	15–45	S	C	24°S–42°S
<i>Parvanachis isabellae</i> (d’Orbigny, 1839) ¹	E	Ep	10–65	S	C	30°S–54°S
<i>Costoanachis sertulariarum</i> (d’Orbigny, 1839) ¹	E	Ec	0–20	S	C	35°N–54°S
<i>Turbonilla argentina</i> [121]	E	Ec	18–57	S	C	35°S–41°S
<i>Turbonilla paralaminata</i> [122]	E	Ec	30–65	S	C	39°S–41°S
<i>Chrysallida multituberculata</i> [122]	E	Ec	30–65	S	C	40°S–46°S
<i>Siphonaria lessoni</i> [123]	E	Ep	0	H	He	32°S–55.22°S

Ep, epifaunal; *I*, infaunal; *Ce*, cemented; *Ec*, ectoparasite; *H*, hard; *S*, soft; *M*, mixed; *C*, carnivorous; *D*, detritivorous; *He*, herbivore; *Sf*, suspension feeder; *O*, oligohaline (3–8‰); *M*, mesohaline (8–18‰); *P*, polyhaline (18–30‰); *E*, euhaline (>30–35‰).

¹The references of species are found on MolluscanBase eds (2021).

Table 3.
Ecological requeriments and distribution of gastropods.

beaches of area D are larger often exceeding hundreds of meters wide. There are two types of beaches regarding the granulometry: a low intertidal sector of fine to medium sand with high distal sectors of gravels, organogenic in composition, and a low intertidal sector and high distal one of fine-medium sand. Both are associated with high energy environments where the malacological associations are mostly euryhaline, of sandy substrate, with less proportion of fauna of scattered rocky substrate. There is one exception, the modern beach of Villa 7 de Marzo which has a particular feature, fine sand substrate with abundance of two bivalves *Plicatula gibbosa* and *Ostrea puelchana*, and the gastropod *Crepidula*, which could be due to the influence of the Negro River. This is also observed in the southern area of this river, in El Cóndor Beach, which has a similar environment and the same mollusks. The modern malacofaunal associations bear 33 to 50% of warm water species in regions A-C, and 31% in area D.

In area D, all the analyzed sites of MIS 7 correspond to paleobeaches. They are currently represented by coastal platforms, of high energy, with mostly euryhaline malacofaunal associations of sandy substrate and subordinated rocky substrate. Respect to the indicators of sea water temperature, these associations are formed only by 20% of warm water bivalves, although it is recorded the gastropod *Tegula atra*, probably indicator of warm water.

In MIS 5e there is a slightly higher proportion of associations of warm waters (27%) with respect to the previous interglacial, being conspicuous the presence of *Anomalocardia brasiliana* and *Tegula atra*, the first one an excellent paleoindicator, and quite probably also the second one.

In MIS 1 the associations of warm water are in lesser proportion than those of MIS 5e (18%), being outstanding the record of *Mesodesma mactroides*. The bivalves *Aulacomya atra*, *Retrotapes exalbidus*, *Ameghinomya antique* and the gastropods *Fisurella radiosa radiosa* and *Crepidula dilatata* are recorded in the beaches of Río

Negro Province. These species have not been described in the modern marine malacofauna of areas A-C (**Figures 3–6**).

4.3 Warm water bivalves and gastropods

4.3.1 Interglacials $\geq$ MIS 9 and MIS 7

These two interglacials recorded in area D were not recorded in the northeast of BAP. In areas A-C, a total of nine species of mollusks were recorded in the

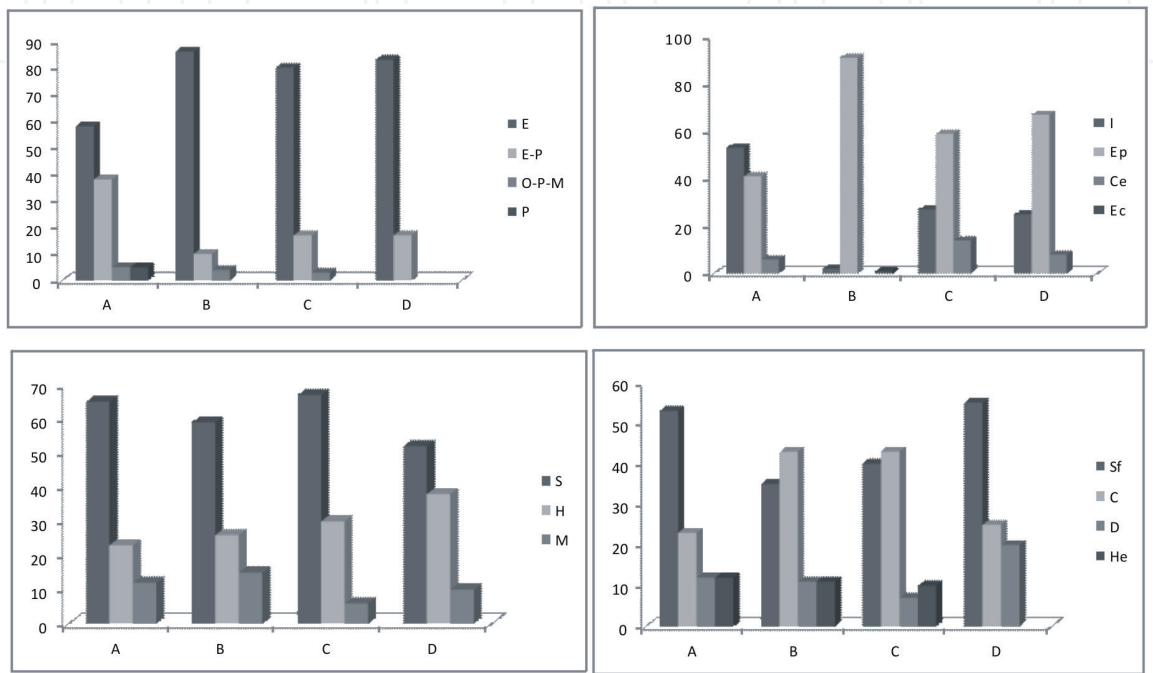


Figure 3.
Paleoecological features of all regions (A–D) in interglacial MIS 5e.

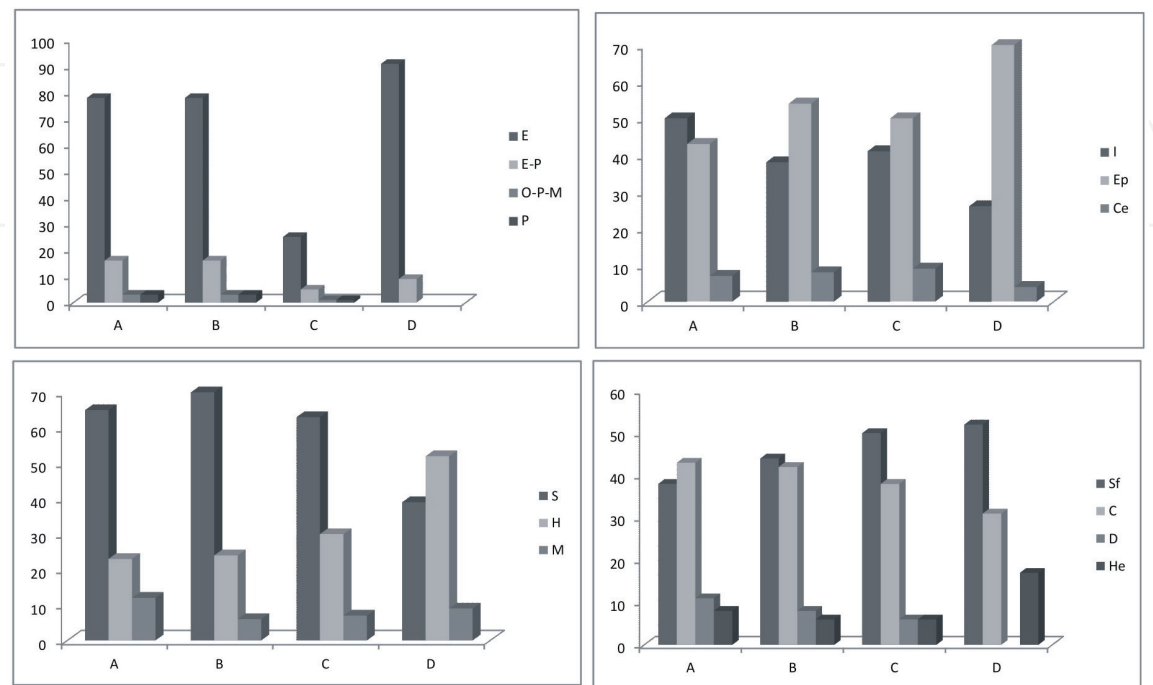


Figure 4.
Paleoecological features of all regions (A–D) in interglacial MIS 1.

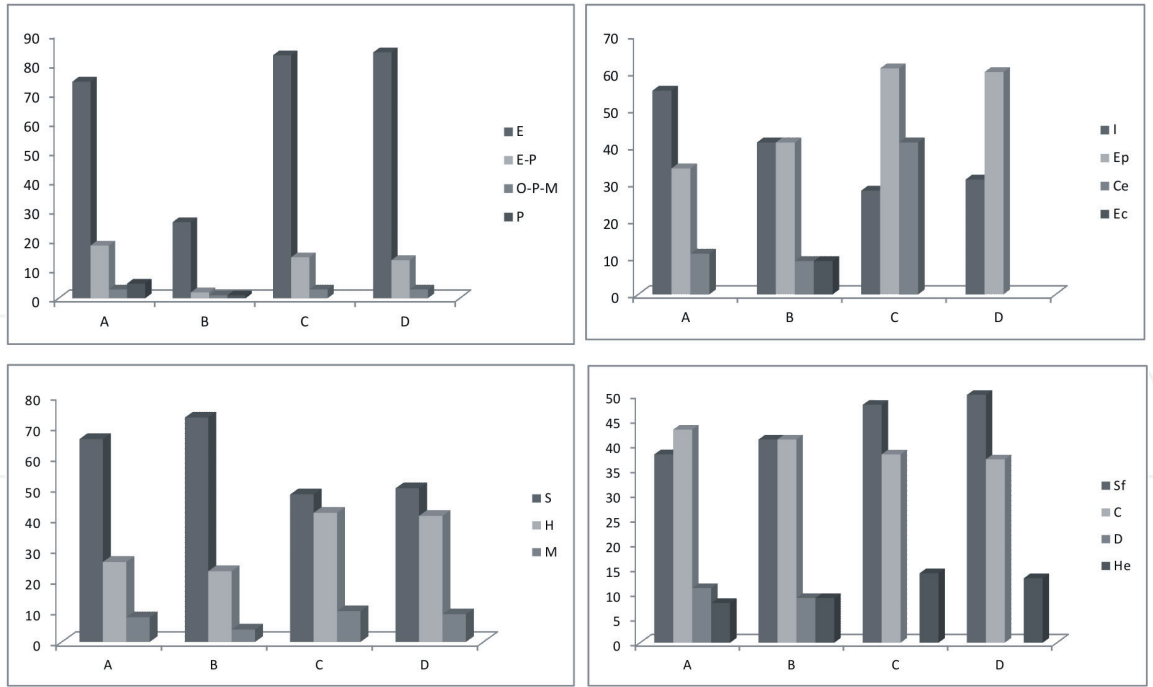


Figure 5.
Paleoecological features of all regions (A–D) in modern beaches.

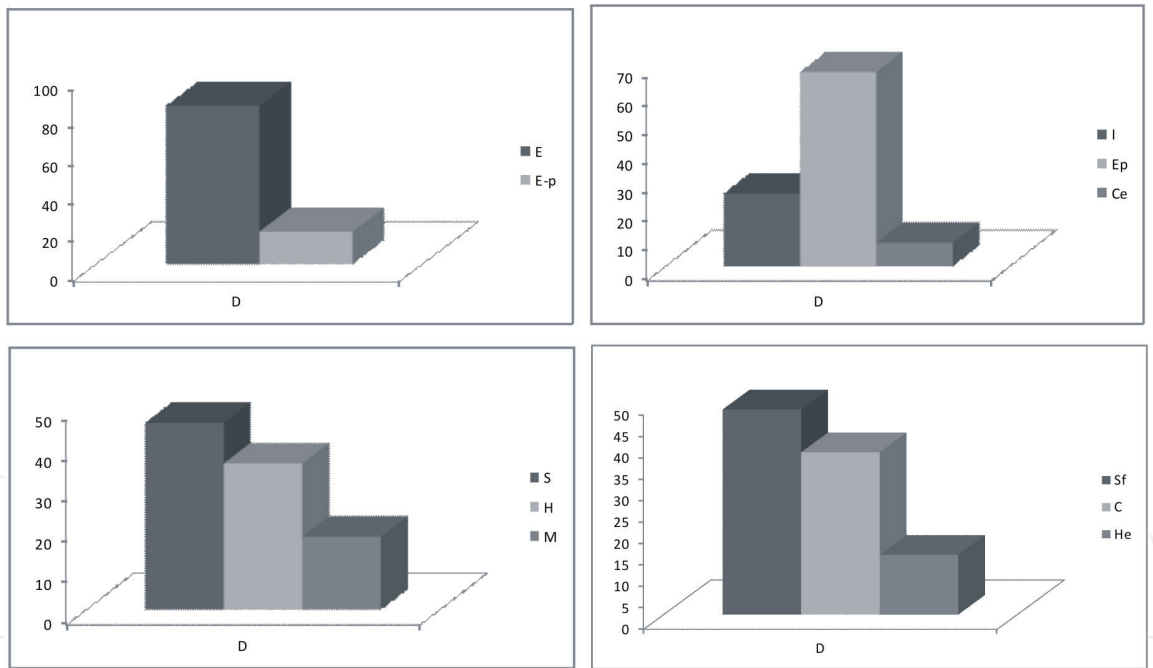


Figure 6.
Paleoecological features of region D in interglacial MIS 7.

Interglacial $\geq$ MIS 9, and among them, there is 50–67% of warm water species of bivalves, being this the oldest record of marine mollusks for the BAP. In MIS 7 analyzed in area D, a total of 11 species was recorded with 20% of warm water bivalves. Most recorded species in both interglacials still inhabit the modern coasts of Argentina, except for the gastropod *Tegula atra*, absent since the MIS 1.

Both interglacials ($\geq$ MIS 9 and MIS 7) revealed the presence of warm water mollusks which are not recorded in the marine deposits of the northeast of BAP where these deposits have not been preserved [124]. The record of these interglacials in the BAP is a novelty in the analysis of gastropods and

bivalves. Whereas Aguirre et al. [27, 28] reported that in the coasts of southern Patagonia, in areas such as Bahía Vera-Camarones (44.2° to 45°S) and Bahía Bustamante-Caleta Olivia (44.9°–45.3°S, Chubut Province, Argentina), the environmental conditions (substrate, depth, and energy conditions) during the late Pleistocene (MIS 7 and MIS 5e) suggest SST similar to those of the modern littoral and even slightly higher than present, recording faunas of warm to temperate waters.

4.3.2 Interglacial MIS 5e

In the marine deposits of this interglacial in area D, 44 molluscan species (25 bivalves and 19 gastropods) were recorded. These deposits are represented by littoral ridges and tidal plains along the south of the BAP coast, and by littoral ridges along area D, with scarce content of calcium carbonate, favoring the record of mollusks. In area C the associations of MIS 5e and MIS 1 have respectively 34 and 33 species. This similarity was also found in area D, in which 22 species were recognized for MIS 5e and 23 for MIS 1. Unlike area D, the mollusks of MIS 5e of the northeast of the BAP are characterized by less abundance and diversity of species related to those of the Holocene MIS 1 [32]. This could be due to a less representation of the Interglacial MIS 5e, and because most valves and shells of Pleistocene deposits are dissolved and/or crystallized, preventing the species identification.

Between 50 and 44% of warm water species of bivalves recorded in the Interglacial MIS 5e of area D, are represented in areas A-C, whereas this relationship is only 27% of the species from area D. Warm water mollusks were recognized in the study area, among the most prominent species of this interglacial, in areas A-C, is the bivalve *Crassostrea rhizophorae* (Figure 7A). This is a warm lineage species that inhabits currently the Caribbean, Venezuela, Surinam, and Brazil up to Uruguay, but is not recorded in the present Argentine coast. However, it is recorded as fossil in the northeast and south of the BAP in the MIS 5e (e.g., [33, 125]).

Another warm lineage species found in area D, is the bivalve *Anomalocardia brasiliiana*, recorded in the area north of the Negro River (Figure 7B). This is the most austral record of the species in the Argentine coast. This species is distributed currently from the French Antilles (18°N) up to the coasts of Brazil (33°S), being an infaunal surface species able to support wide salinity ranges (e.g., [126, 127]).

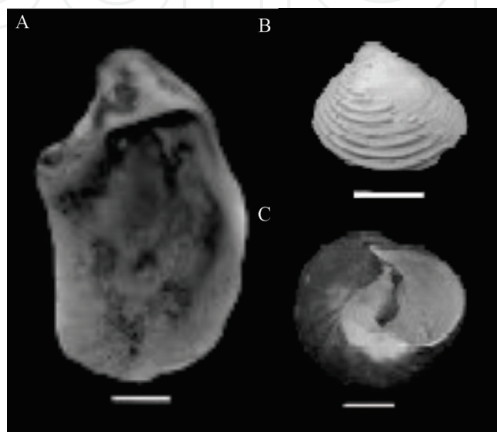


Figure 7.
The warm species of Pleistocene. (A) *Crassostrea rhizophorae* (Guilding) (MLP: 34.012, MIS 5e, region B), (B) *Anomalocardia brasiliiana* (Gmelin) (CEGH-UNC: 25.609, MIS 5e, region D) and (C) *Tegula atra* (Lesson) (CEGH-UNC: 25.615, MIS 5e, region D).

As fossil, it was found in Uruguay, both in the MIS 5e of the Nueva Palmira Formation [43] and in the Holocene of the Villa Soriano Formation [128]. In Argentina, this species is reported for marine deposits within the Pampiano Formation of Lomas de Zamora (34°46'S, northeast of BAP; [129]), as well as in the localities of Magdalena, Punta Piedras (BAP) and south of Entre Ríos Province [124]. This species was found in the Pleistocene deposits of Bahía Blanca (south of BAP) together with *Crassostrea rhizophorae* [33].

Tegula atra is distributed in intertidal and subtidal shallow rocky substrates, up to 6 m depth (**Figure 7C**) [130]. It is among the most abundant species of the Pleistocene of area D, and is well preserved in deposits of MIS 7 and MIS 5e [5] but it is not recorded in deposits of MIS 1. Whereas in the Pacific coast, *Tegula atra* is recorded in the late Pleistocene and Holocene deposits of the northern and southern coast of Peru (e.g., [131, 132]). In Chile, it is recorded in late Pleistocene deposits of Caleta Coloso (23°45'S/70°28'W), north and south of Antofagasta (23°37' S) [45], as well as in archeological sites such as the late Pleistocene-middle Holocene of Quebrada de Lazareto (south of Chile) [133], middle and late Holocene of the IV Region, Los Vilos (e.g., [134]) and Holocene deposits of the Magellan Strait [135]. *Tegula atra* is currently distributed in the Pacific coasts from Pacasmayo (7°24'S, Peru) up to the Magellan Strait (53°S) [136], but there is no evidence of living specimens in the south Atlantic coasts.

4.3.3 Interglacial MIS 1

A total of 58 species (31 bivalves and 27 gastropods) was recorded in the marine malacofauna of the Interglacial MIS 1 of northern Patagonia (areas A-D), which differs from the northeast of BAP where Aguirre [89] reported a total of 62 species (25 bivalves and 37 gastropods). Concerning the molluscan composition, in the northeast of BAP, gastropods are more abundant than bivalves both in number of species and of individuals. As a comparison, among the regions studied, area A recorded 51 species (29 bivalves and 22 gastropods), and area B 49 species (25 bivalves and 24 gastropods), being in both regions, bivalves more numerous than gastropods. Whereas in area C, 34 species (17 bivalves and 17 gastropods) were recorded, unlike area D where 42 species (20 bivalves and 22 gastropods) were recorded, being in this latter the number of gastropods slightly higher than bivalves.

The marine deposits of MIS 1 in areas A-C are formed by tidal plains and littoral ridges. Tidal plains yielded mainly *Tagelus plebeius* among bivalves and *Heleobia australis* among gastropods. These species support variable salinity, being recorded in oligohaline–mesohaline–polyhaline associations (salinity between 3 and 30 gr/l), typical of low energy environments, most of them with low diversity indexes. In the littoral ridges, the diversity indexes are mostly higher than those of tidal plains. They yielded among bivalves *Pitar rostratus*, *Amiantis purpurata*, *Ostreola equestris*, and among gastropods *Buccinanops cochlidium* and *Heleobia australis*, typical of high energy environments.

The marine deposits and their malacofauna in the northeast and south (areas A-C) of the BAP are similar in the two types of deposits of the Interglacial MIS 1. The tidal plains are represented in regions A-C and are related to the development of the Colorado River and Bahía Anegada. The most common species are *Heleobia australis*, *Tagelus plebeius* (in life position) and *Corbula patagonica*, being similar to the marine malacofauna of the northeast of the BAP of the Canal 18 Member of the Las Escobas Formation (Holocene, MIS 1) and the estuarine facies of the Mar Chiquita Formation (**Figure 8**).

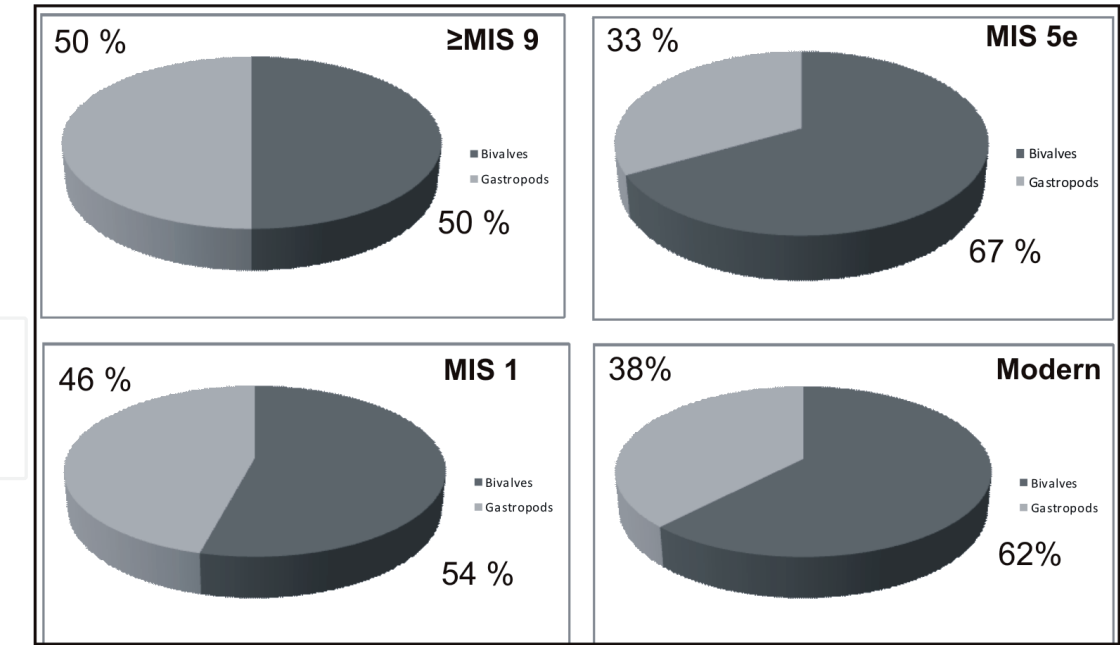


Figure 8.
Warm water vs. cold water during the quaternary in all regions (A–D).

5. Final comments

In the last 400.000 years there were variations in the molluscan paleocommunities of north Patagonia (southern BAP and north of Río Negro Province). The marine malacofauna of this area is composed by two associations, the first one is formed by Holocene sites with abundance of *Heleobia australis* and *Corbula patagonica*, and the other, mainly by Pleistocene sites and modern beaches with *Amiantis purpurata* as the most abundant, together with *Buccinanops globulosus*, *Bostrycapulus odites* and *Tegula patagonica*. The record of *Crassostrea rhizophorae*, *Anomalocardia brasiliiana* and *Tegula atra*, in north Patagonia suggests that the interglacials MIS 7, MIS 5e and MIS 1 were slightly warmer than today. These latter species, except for *Tegula atra* live today in lower latitudes. However, the associations determined for the analyzed interglacials did not change concerning the faunal composition as a whole, and, except for the latitudinal changes of the three species mentioned above, and the record of temperate to cold water associations since the Interglacial MIS 1 in north Río Negro Province (ecotone), the composition remained similar, showing only changes in abundance of species.

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