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Palaeogeography, Palaeoclimatology, Palaeoecology 229 (2006) 251–286

PALAEO

www.elsevier.com/locate/palaeo

Palaeoenvironments and palaeoclimates of the Quaternary molluscan faunas from the coastal area of Bahía Vera-Camarones (Chubut, Patagonia)

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Received 18 February 2004; received in revised form 1 June 2005; accepted 16 June 2005

Abstract

Quaternary molluscs are useful tools as indicators of environmental and climatic changes through time. The Patagonian coastal area exhibits a series of Quaternary marine terraces (MT) at various elevations with a well-preserved molluscan fauna. The assemblages from Mid– to Late Pleistocene and Holocene raised beach deposits exposed between Bahía Vera and Bahía Camarones (44.2°S–45°S) were examined, and systematic, palaeoecological and palaeobiogeographical aspects were reviewed and updated in terms of interpretation of the littoral area and biotic responses to climate changes. Collections at 10 fossiliferous localities and four modern sites of the adjacent nearshore show that molluscs (41 taxa: 24 gastropods and 17 bivalves) represent 91% of the total faunal content. Identification of the typical taxa for at least four sea-level highstands was based on the occurrence, relative abundance, species richness, and diversity indices (Margaleff's; Sannon Weaver's). Variations between terraces MTIII (Camarones, higher than +30 m, probably ca. 400 ka), IV (Punta Pescadero and Camarones,+22–29 m, 178–239 ka), V (Bahía Vera, Punta Pescadero, Camarones,+16–18 m, 92–135 ka) and VI (Punta Lobería, Punta Pescadero, Camarones,+6–12 m, 2.5–8 ka) add to a better understanding of palaeoenvironments and palaeoclimates linked to sea-level highstands since MOIS11. Their original habitat was typical of rocky-shore, high-energy and euhaline waters, similar to the modern conditions of adjacent benthic communities. The most characteristic taxa are: *Patinigera* deaurata (Gm.), *Fissurella* spp., *Crepidula protea* d'Orb., *C. aculeata* (Gm.), *C.* cf. *unguiformis* Lam., *Natica isabelleana* d'Orb., *Trochita pileus* (Lam.), *Buccinanops* spp., *Pareuthria plumbea* (Philippi), *Acanthina monodon* (Pallas) and *Trophon* spp. (Gastropoda); *Brachidontes purpuratus* (Lam.), *Protothaca antiqua* (King), *Clausinella gayi* (Hupé), *Mactra* aff. *patagonica* (d'Orb.) and *Ostrea tehuelcha* (Feruglio). New records in this area for the Late Pleistocene are: *C. aculeata* (Gm.), *C. onyx* Sow., *C. protea* d'Orb., *T. patagonica* (d'Orb.), *N. isabelleana* (d'Orb.), *B. rodriguezi* (d'Orb.), *A. tehuelchus* (d'Orb.) and *C. gayi* (Hupé). *Ostrea tehuelcha* d'Orb. became extinct and *Tegula atra* (Lesson), *N. isabelleana* (d'Orb.), *B. rodriguezi* (d'Orb.), *C. patagonica* (d'Orb.) and *D. vilardeboana* (d'Orb.) migrated into the area. Exclusive for MTIII (MOIS11) are *Pectinidae* indet., *Ostrea tehuelcha* and *Mactra* cf. *patagonica* d'Orb. which, together with other taxa (i.e., *Corbula patagonica*, *Diplodonta vilarde-*

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0031-0182/$ - see front matter
doi:10.1016/j.palaeo.2005.06.025

boana), suggest warmer sea surface temperature (SST) than at present. Typical of MTIV (MOIS7) are *T. atra*, biggest *P. antiqua* (King), and Veneroida indet. The assemblage from MTV (MOIS5c?, 5a?), *T. atra*, *T. patagonica*, *C. dilatata* Lamk., *M. edulis* Linn., *B. purpuratus*, *P. antiqua*, and *P. rostratus* (Koch), is not indicative of a climatic optimum and thus of the Last Interglacial maximum highstand (MOIS5e). MTVI (MOIS1) is characterized by *B.* cf. *purpuratus*, *N. (Patinigera) magellanica* (Gm.), *N. (P.) deaurata* (Gm.), *Trophon geversianus* (Pallas), *B. purpuratus*, and *Aulacomya atra* (Molina). *N. delicatissima* (Strebel), *Chlamys* sp., *Panopea abbreviata*, and *Lyonsia* sp. exclusively occur in the modern nearshore. According to the global isotope curve, MOIS5e highstand (125 ka BP) was the warmest since the Mid-Pleistocene. The innermost MTIII assemblage provides an opportunity to hypothesize that along the eastern coast of South America the corresponding highstand (probably MOIS11, ca. 400 ka BP ?) belongs to the warmest of the Pleistocene interglacials preserved, as proposed earlier for the Chilean coast (Ortlieb et al., 1996). This assemblage could be correlated with the Belgranense of the Bonaerensian littoral. The Holocene Climatic Optimum (5–8 ka) is confirmed to have influenced the littoral biota. A slightly higher SST (1–3 °C) implied atmospheric and palaeoceanographic changes, with a southwards shift of the dominant warm (Brazilian) and cool (Malvinas = Falkland) currents along the SWAtlantic and, consequently, of the Argentinean and Magellanean marine zoogeographical provinces.

Keywords: Molluscs; Marine Quaternary; Patagonia; Palaeoenvironments; Palaeoclimates

1. Introduction

The Quaternary sea-level history of Argentina has been explained by several factors (eustasy, sediment supply, wave action, current energy, hydro-isostatic tilting following deglaciation). In Patagonia, sea-level changes allowed the preservation, along the coastal area, of a series of raised marine shorelines at different elevations, a complex of fossiliferous coastal deposits known as "*Marine Terraces*" (Feruglio, 1950) (Table 1). They contain a very rich macrofauna mainly of molluscan shells.

Four series of terraces (MT) exposed along southern Chubut Province between Bahía Vera and Bahía Camarones (44.2–45°S) (Fig. 1), formed in response to global sea-level highstands and minor neotectonic events, are very well preserved and adequate for palaeontological studies. The molluscan shells occur associated with other macroinvertebrates (balanids, terebratulid brachiopods, polychaetes, bryozoans, corals) and represent parautochthonous shell concentrations with distinct taphonomic signatures. It can be expected that molluscs provide palaeoenvironmental signals complementary of detailed sedimentologic and modern geochronological work performed in the same area (Schellmann and Radtke, 2000; Rostami et al., 2000), as has been shown for nearby regions (Aguirre, 2003; Aguirre et al., in press).

In the study area little work has been done on the benthic assemblages, and the gastropods and most of the bivalves have not as yet been sufficiently analysed, although their study is very important to understand the general palaeoenvironmental conditions of MOIS (marine oxygen isotope stages) of the current global isotope curve (Haq et al., 1987) linked to sea-level episodes. The aim of this paper is to present an update of palaeoecological, palaeobiogeographical and palaeoenvironmental aspects based on the whole molluscan fauna of geographically and stratigraphically well constrained Quaternary littoral deposits.

The number, timing, duration and climate (sea surface temperatures, SST) of the Quaternary sea-level highstands preserved in Argentina need further studies, complementary of recent work performed on the coastal area and continental shelf (e.g., Parker et al., 1996, 1999; Violante and Parker, 1999; Guilderson et al., 2000; Peltier and Rostami, 2000). From a palaeontological point of view, to establish molluscan records characteristic of former marine episodes linked to shifts in oceanic and atmospheric circulation patterns during highstands of the last 400 ka, comparisons between Pleistocene interglacials and the Mid-Holocene transgression, and eventual biotic responses to the Holocene Climatic Optimum still need to be studied. In addition, the area provides an opportunity to test whether, based on the molluscan fauna, the oldest Pleistocene terrace (MOIS11?, 362–423 ka ?) represents a longer and warmer episode than the successive interglacials preserved on

Table 1
Stratigraphical interpretation of the study area by previous authors

	SURINAM	BRAZIL	URUGUAY	ARGENTINA											
				BONAERENSEAN LITTORAL			PATAGONIA								
				SAMBOROMBON BAY	MAR CHIQUITA	BAHIA BLANCA	*"TERRAZAS MARINAS" (Marine Terraces)*	AGES (AAR - ESR)	CHUBUT				SANTA CRUZ		
									CAMARONES	BAHIA BUSTAMANTE	BAHIA SOLANO	COMODORO RIVADAVIA	CALETA OLIVIA	PUERTO DESEADO	PUERTO MAZAREDO
	Altena, 1969, 1975	Martin and Suguio, 1992; Martin al., 1993	Sprechmann, 1978; Martínez et al., 2001	Fidalgo, 1979	Fasano et al., 1982	Farinati, 1985; Chaar and Farinati, 1992	Feruglio, 1950	Rutter et al., 1989, 1990 Schellmann & Radtke, 2000	Feruglio, 1950; Camacho, 1979; Codignotto, 1983; Rutter et al., 1989-1990; Shellmann & Radtke, 2000; Rostami et al, 2000	Feruglio, 1950; Cionchi, 1987; Rutter et al., 1989-1990; Shellmann & Radtke, 2000; Rostami et al,	Codignotto, 1983	Feruglio, 1950; Rutter et al., 1989-1990	Feruglio, 1950; Codignotto, various	Feruglio, 1950; Rutter et al., 1989-1990	Feruglio, 1950; Codignotto et al., 1987; Rutter et al., 1989-1990
HOLOCENE	Holocene transgression	Holocene transgression	VIZCAINO Fm. = V.Soriano Fm. (+3 m)	LAS ESCOBAS FM. Cerro de la Gloria (+ 5 m) Canal 18 DTO.R.SALADO FM.	MAR CHIQUITA FM. Marine facies Estuarine facies	POST-GLACIAL TRANSGR	VI Comodoro Rivadavia (+–612 m)	YOUNG	Littoral Ridges + 6-12 m (ca. 4-7.5 Ka)	ZANJON EL PINTER FM. + 8–10 m D/L 0.21– 0.29 ^{14}C (2030 – 8950)	Littoral Ridges + 2 –15m (ca. 2–6 Ka)	Marine T VI (+8–12 m)	Marine T VI (+8–10 m) (6940)	Marine T VI (+8–10 m) (6940)	Marine T VI +8–10 m (500–5850; 9520)
PLEISTOCENE		Pleistocene transgression (123 ka+ 8–10m); Pleistocene transgression (> 123 ka +13–25m)	CHUY FM. (+1–4 m) (29.5–35.5 ka) 5e	PASCUA FM. (+3–10m) (> 30–35ka) 5e ?		INTERGL. SANGAMON ? + 12-14 m)	V Puerto Mazaredo (+15-30 m); IV Puerto Deseado (+30–40 m); III Camarones (+40–95 m)	INTER-MEDIATE Last Interglacial IS 5e; OLD Pre-Last / Penultimate Interglacial IS 7 or 9 ?	MT V (+ 22–26 m); TEHUELCHE FM. ?; MTIII (+ 35–40 m)	CALETA MALASPINA FM. (+25-29 m) 36-37 Ka D/L 0.74 ESR 116-195; (+ 34–41 m) D/L 0.73–0.81; ESR 219->356 BP IS 7 or 9 ?			Marine T V ? (+ 20–25 m) min 30–35ka IS 5 e ?; Marine T IV (+ 30–40 m) ESR > 249 BP IS 7 or 9 ?	Marine T V ? (+ 20–25 m) D/L 0.57 IS 5 e ?; Marine T IV (+ 30–40 m) D/L 0.66 ESR > 249 BP IS 7 or 9 ?	Marine T V (+ 15–30 m)

Symbols:

Ka: 1,000 yrs B.P.
ESR: dates from Rutter et al., 1989, 1990; Schellmann & Radtke, 2000
IS: Isotope Stage or substage

Full source of data on: Feruglio,1950; Fidalgo,1979; Codignotto,1983,1984; Codignotto et al.,1987; Rabassa,1987; Rutter et al., 1989, 1990; Aguirre,1993; 2003;Schellmann & Radtke, 2000; Rostami et al., 2000.

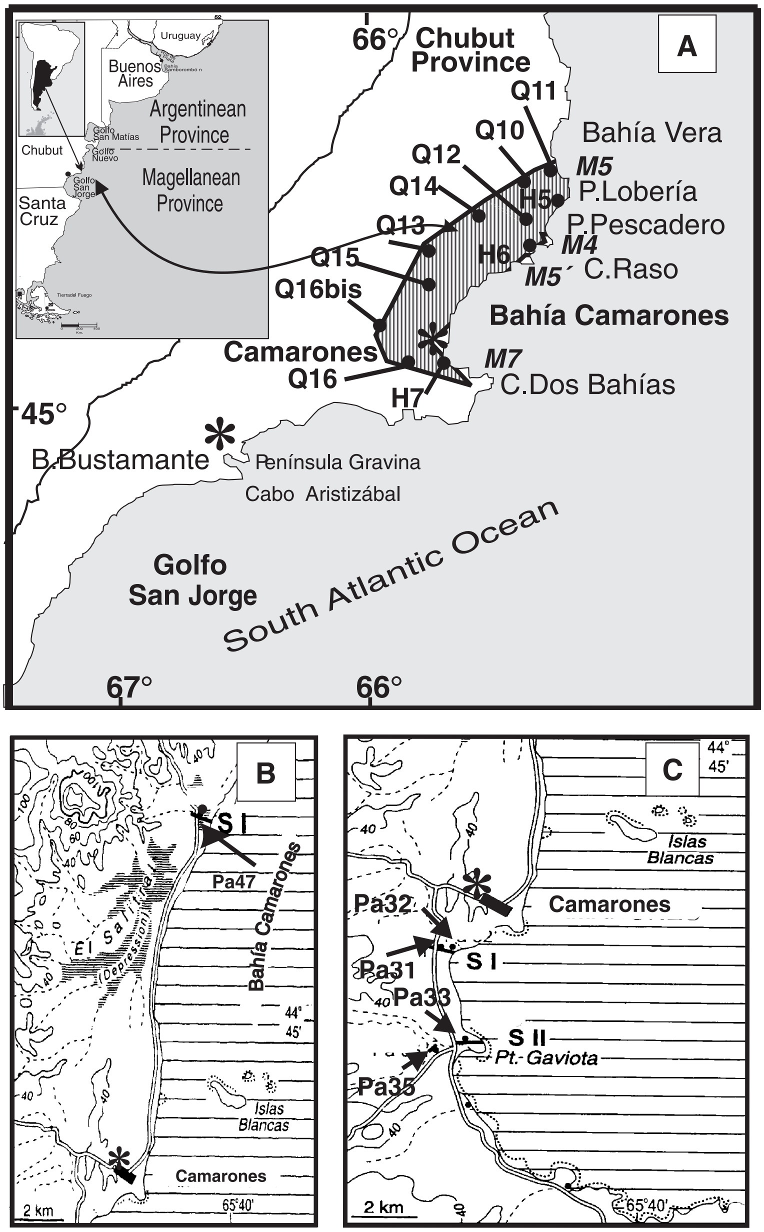


Fig. 1. Area of study in central Patagonia (Argentina) along the coastal region of the southern Chubut Province (SW Atlantic). A, general location of fossiliferous sites along Bahía Vera– Bahía Camarones coastal area (Chubut Province, Patagonia, Argentina, Southwestern Atlantic). Molluscan samples for palaeontological analysis from Holocene (H) and Pleistocene (Q) deposits and modern samples of shells collected along the adjacent littoral (M) (modified from Aguirre, 2003). B and C show the position of the samples analysed for dating of the ridge systems along the same area after Schellmann and Radtke (2000) north (B) and south (C) of Camarones (samples used for palaeoenvironmental inferences in this study were selected whenever possible from approximately the same sites in order to make comparisons referable to the dates available). The deposits sampled correspond to the “marine terraces” of the local literature (MT; sensu Feruglio 1950, p. 89). Figs. B and C are modified (ca. 95%) from Schellmann and Radtke (2000) where SI and SII refer to the location of their cross-sections and samples (Pa 47, Pa32, Pa31, Pa33, Pa35) mentioned here (Table 2).

land (Burckle, 1993; Ortlieb et al., 1996a; Kukla et al., 1997, 2002).

Along central Patagonia, it is especially relevant to compare the molluscan assemblages and palaeoenvironments of the Last Interglacial vs. the Mid-Holocene transgression and to address the problem of correlation of the Pleistocene marine terraces with the Pleistocene beach deposits preserved northwards along the Bonaerensian coastal area (Pascua Fm., Belgranense; Río de La Plata margin to Bahía Blanca) (Table 1).

This study is part of a major project which aims at improving our knowledge of the Argentinean molluscan faunas to improve interpretations of the nearshore environment since the Mid–Late Pleistocene to present. An attempt is made to characterize the typical molluscan taxa for different highstands and, on this basis, to suggest their palaeoeclimatic conditions. This is essential for future studies on the biogeographic history and origin of the modern molluscan faunas from the southwestern Atlantic Ocean, which have not yet been deciphered.

2. Previous studies

The deposits and faunas analysed are known in the literature since the classical monographic contributions by D'Orbigny (1834–1847),Darwin (1846) and Feruglio (1933, 1950). Various modern studies have examined coastal terrace sequences, raised beach ridges, and the molluscs preserved, with a view to determining geomorphological, sedimentological and chronostratigraphic characteristics of the coastal deposits and of the Argentine continental shelf. Among most recent authors dealing with these aspects are Rutter et al. (1990), Codignotto et al. (1992), Peltier (1998), Schellmann and Radtke (2000), Rostami et al. (2000), and Guilderson et al. (2000). According to the dating available, the Quaternary MT originated during the post-glacial marine transgression (MOIS1) and during at least three Pleistocene highstands (MOIS9 or older, MOIS7 and MOIS5) (Fig. 2, Table 1).

The available data on the molluscan faunas from the Quaternary MT of Patagonia in relation to sea-level changes, including some of our deposits or nearby sites, mainly refer to general palaeontological aspects, and in some cases are based on bibliographic compilations only (Feruglio, 1950; Gordillo, 1998; Aguirre and Codignotto, 1998; Pastorino, 2000). Additional information refers to the Argentine continental shelf during the Quaternary (Richards and Craig, 1963).

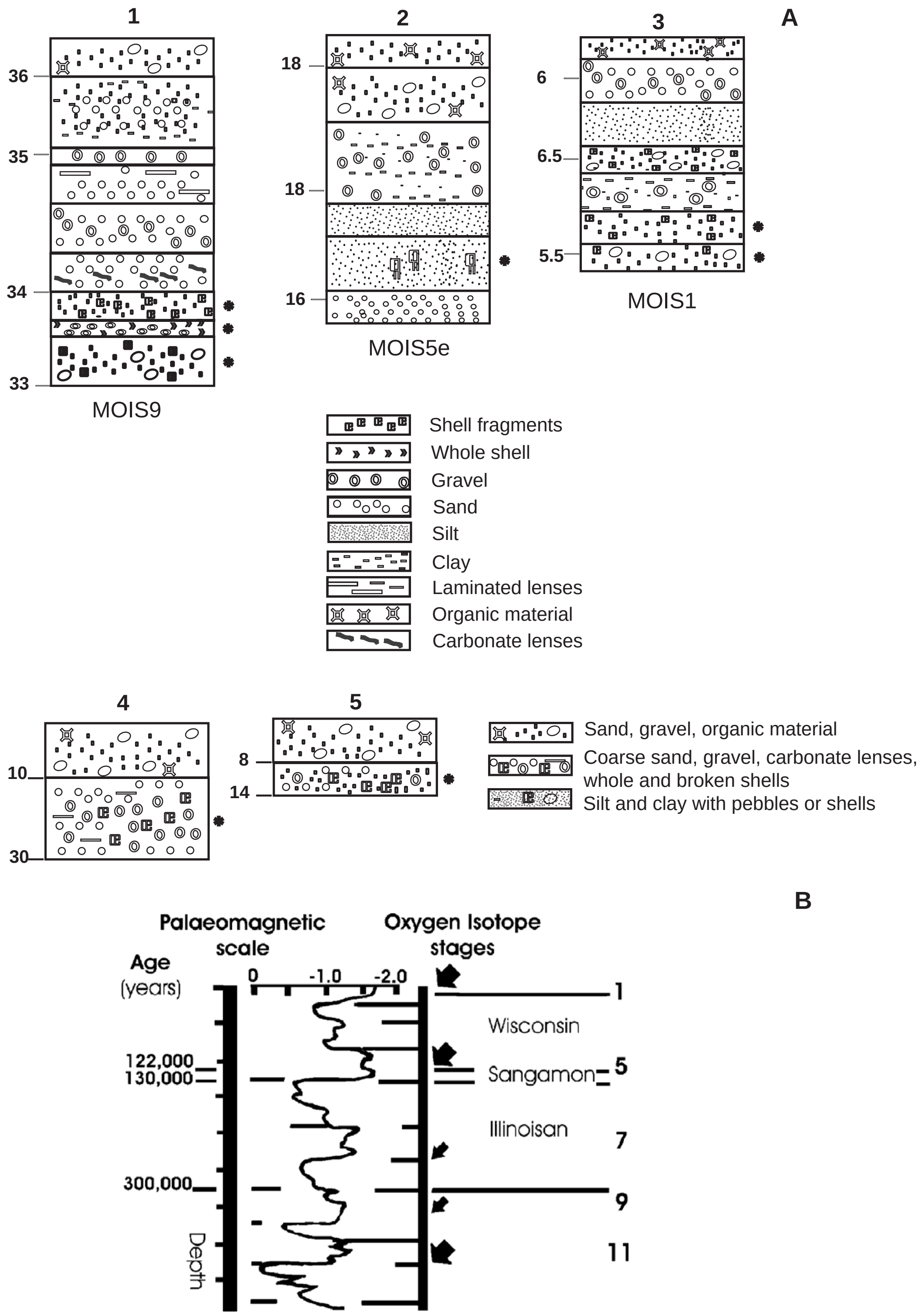
Stable isotope analyses ($\delta^{18}O$ and $\delta^{13}C$) on molluscan shells from the terraces studied have not as yet been performed. A preliminary analysis has been initiated on *Protothaca antiqua* (King), *Brachidontes purpuratus* (Lamk.), *Patinigera magellanica* (Gm.), and *Buccinanops globulosus* (Kiener) from the modern littoral at Golfo San Jorge (Comodoro Rivadavia and Bahía Lángara) (Aguirre et al., 2002). It will serve future comparisons with Holocene and Pleistocene shells of the same taxa from the MT studied here.

This contribution complements previous work performed in Patagonia southwards of the study area along the Bahía Bustamante area (Aguirre et al., in press) and along the Golfo San Jorge (Aguirre, 2003), and northwards along the Buenos Aires Province (Aguirre, 1993). Overall, these studies form parts of a broader project concerning the Quaternary molluscan faunas from the coastal area of Argentina, between the Río de La Plata down to the southern Santa Cruz Province (Fig. 1).

3. Regional setting

The coastal sector studied extends along the SE Chubut Province, between Bahía Vera and Bahía Camarones (Fig. 1), where four main series of regressive, pebbly, raised elongated beach ridge systems of the Mid to Late Pleistocene and Holocene are preserved. They are composed of sediment with whole and fragmented shells and run for about 25 km subparallell to each other, following the configuration of the modern coastline, at different elevations above present sea-level. They are 2–4 km wide and the distance to the ocean is generally 1–3 km.

All along this coastline the Holocene shorelines are lower than the Pleistocene terraces (Fig. 2), and Pleistocene deposits at different altitudes may have the same or different ages. These, like other Quaternary coastal deposits in Patagonia, were tectonically uplifted, their height above present mean sea-level showing a northwards decreasing trend. Their origin


A
1
36
35
34
33
MOIS9
2
18
18
16
MOIS5e
3
6
6.5
5.5
MOIS1
Shell fragments
Whole shell
Gravel
Sand
Silt
Clay
Laminated lenses
Organic material
Carbonate lenses
4
10
30
5
8
14
Sand, gravel, organic material
Coarse sand, gravel, carbonate lenses, whole and broken shells
Silt and clay with pebbles or shells
B
Palaeomagnetic scale
Oxygen Isotope stages
Age (years)
0
-1.0
-2.0
122,000
130,000
300,000
Depth
Wisconsin
Sangamon
Illinoisan
1
5
7
9
11

was explained due to plate tectonic processes linked to mantle connective circulation (Rostami et al., 2000).

The exterior ridge (+6–12 m above m.s.l.) is composed of gravel and loose sand with mostly whole and very well preserved shells; the second (+16–18 m above m.s.l.) is composed of sand, gravel and pebbles with shells, sometimes cemented by carbonate; the third one (+24–29 m above m.s.l.) of gravel and shells, often locally cemented; the oldest and innermost ridge (over +40 m above m.s.l.) lies on a pyroclastic deposit and is composed of gravel and pebbles with highly cemented, often fragmented shells.

Feruglio (1950) first described in this area a pattern of MT: an inner ridge at +40 m above m.s.l. as MTIII, intermediate ridges at +28–40 m as MTIV, and at +20–26 m above m.s.l. as MTV, and the most exterior ridge at +10–12 m above m.s.l. as MTVI. More recently, they were assigned by Radtke (1989) a Middle Pleistocene, Last Interglacial and Holocene age, respectively. The ages (ESR, Th/U) obtained by Schellmann and Radtke (2000) for the Pleistocene terraces suggest at least three marine highstands which they interpreted as MOIS9 ?/11 (342–400 ka), MOIS7 (225 ka), and MOIS5 (125 ka) (Table 2).

These authors and Rostami et al. (2000) provided detailed descriptions of the unconsolidated marine deposits associated with sea-level changes in the study area. According to them four types of features can be recognized: 1) terraces with recycled materials, polished whole and broken molluscan shells, from different sources and altitudes; 2) storm beach deposits with washed shells originated by wave action behind or at the inner margin of the beach above spring tide or at ordinary sea-level; 3) ridges with fragmented and, less commonly, complete shells found above the water level on the foreshore; 4) bars represented by low ridges of sand with shells washed ashore, formed in shallow water adjacent to the coastline by aggradation.

Fig. 2 shows a synthesis of the morphostratigraphy and sedimentology of the oldest interglacial (Middle Pleistocene,+33–35 m, MTIII), a Last Interglacial (Late Pleistocene,+6–17 m above m.s.l., MTV) and the Holocene highstand (+8–10 m above m.s.l., MTVI) with the corresponding isotope stages. The ages obtained by Codignotto (1983, 1988), Rutter et al. (1989, 1990), Schellmann and Radtke (2000) and Rostami et al. (2000) are summarized in Table 2.

3.1. Holocene deposits (MOIS1)

The exterior terrace (MTVI) is exposed at Punta Pescadero, Cabo Raso, and southwards of Camarones consisting of several undulations subparallell to the shoreline and covered by vegetation. It has typically a fresh aspect and is composed of gravel and loose sand with abundant, very well preserved molluscan shells, in most cases retaining their original colour and lustre. The ages of the Holocene littoral terrace (at ca. 6–12 m above m.s.l.) range between 2.5 and 8 ka (samples analysed for Fig. 8 are ca. 4–7/8 ka BP) (Tables 1 and 2) (see also Aguirre, 2002).

According to the ages available, these deposits were undoubtedly formed during MOIS1 at 8 ka B.P., a highstand (ca. 6 m higher than the present sea level). It was controlled by the influence of the hydro-isostatic adjustment following deglaciation and the redistribution of water in the ocean basins due to ice-sheet melting (Rostami et al., 2000). It is the most easily recognized of all the MT along Patagonia, at +6–7 ,+8–9 ,+8–12 m above m.s.l. in Río Negro (San Antonio Fm.), Chubut (Zanjón El Pinter Fm.) and Santa Cruz provinces, respectively (Table 1). It correlates with synchronous deposits northwards in Buenos Aires Province (+5 m above m.s.l.) and with other areas of eastern South America, such as Surinam, Brazil (+0–1 m above m.s.l.) and Uruguay (Villa Soriano Fm., Viz-

Fig. 2. Pleistocene and Holocene sediments at the Bahía Camarones coastal area. A, Profiles of Pleistocene (1, 2) and Holocene (3) marine terraces (MT) redrawn and slightly modified (ca. 90%) from Rostami et al. (2000). Numbers refer to altitude (m). Whenever possible, shell samples include some levels with shells from terraces dated by these authors (marked with *): in column 1 equivalent to PA02H6; in column 2 equivalent to PA02Q12, 15; in column 3, equivalent to PA02Q16). Numbers refer to altitude (m). Columns 4, 5 for sample locations at marine terraces IV (Pleistocene) and VI (Holocene), respectively (numbers refer to depth in cm). B, Isotope curve showing stages of Quaternary high sea-level episodes; arrows indicate highstands and MOIS since the Mid-Pleistocene (1, 5, 7, 9, 11).

Table 2
Dates of samples analysed

Marine terraces (F)	Altitude (+m amsl)	Localities: S Bahía Vera–Camarones (^) samples studied by previous authors	MOIS*	Dating (+)	Samples (this paper)
Modern littoral					M4, M5, M5́, M5 (o), M7
Holocene					
MTVI	+10–12 (F) +8–10 (C) +6–12 (1, 2, 3) +4– 10 (6) +5–6 (7)	H1, H2, Pa31, Pa32, Pa33 5 km N. of Camarones	1	2880 ± 90; 2880+85; 3860 ± 95; 4370 ± 95; 7520 ± 120 (1, 2, 3) 2618 ± 92 (6), 5380 ± 70 – 6708 ± 46 (6) 7 ± 2 (7)	PA02Hol5 PA02Hol6 PA02Hol7
Pleistocene				30,900 ± 1100; 31,800 ± 1400 as minimum ^{14}C (1)	
MTV					
	+22–26 (F)				
	+16–19 (6)		5e		
	+12 – 13 (6)	Pa47c Pa47a		92 ± 9 ka; 99 ± 12 ka; 115 ± 9 ka; 117 ± 13 ka; 131 ± 17 ka; 133 ± 15 ka; 135 ± 18 ka (6)	PA02Q12 PA02Q15
	+16–17 (7)	12 km S. of Camarones		112 ± 13; 115 ± 9; 117 ± 5; 117 ± 6 (Th/U) 110 ± 8; 114 ± 9 ESR) (7)	
MTIV				36,000 ± 2000; 37,000 ± 2400; >43,0000 as minimum ^{14}C (1)	
	+28–40 (F) +20–26 (6) +25–29 (C)	Pa31	7	178 ± 16 ka; 180 ± 22 ka; 196 ± 33 ka; 199 ± 27 ka; 200+40 ka; 209+18 ka; 231+20 ka (6) 158–239 (7)	PA02Q10 PA02Q11 PA02Q14 (PA02Q13)
MTIII					PA02Q16 PA02Q16bis
	+35–40 (C)				
	+33–35 (6)	Pa35	9/11	342 ± 29 ka; 372 ± 30 ka; 378 ± 62 ka; 380 ± 92 ka; 383 ± 38 ka (6)	
	+33–34 (7)	6–7 km S. Camarones	9/11	309 ± 50,000/35,000; 354 ± 45; 338 ± 34 (7)	

References for geomorphology, sedimentology and dating available (+) from previous work performed in the area: F: Feruglio (1950); C: Cionchi (1987). 1: Codignotto, 1983 (^{14}C, most in *Protothaca antiqua*). 2: Codignotto, 1988 (^{14}C). 3: Codignotto et al., 1992 (^{14}C). 4: Rutter et al., 1989, 1990 (D/L, ESR, Th/U; different species). 5: Schellmann and Radtke, 1997 (ESR) (no details about the species dated). 6: Schellmann and Radtke, 2000 (^{14}C, Th/U, ESR) (mostly probably on *P. antiqua* and on unidentified taxa of unknown palaeoecological value or taphonomic history; samples H, Pa). 7: Rostami et al., 2000 (Th/U and ESR; mostly probably on *P. antiqua*, not *Mercenaria*, several in *Mytilus* sp. or in unidentified species). *: estimations for equivalent simples; ^ (from North to South): Bahía Vera, Punta Lobería, Punta Pescadero, Cabo Raso; Bahía Cruz; Bahía Camarones; Bahía Bustamante, Caleta Malaspina (see also Fig. 1). MOIS = Marine Oxygen Isotope Stages/substages. Note that *Mercenaria* is not preserved in this area. The authors probably misidentified the material, which most probably belongs to *Protothaca antiqua* (King).

caíno Fm.) (Altena, 1969, 1975; Martin et al., 1988, 1993; Martin and Suguio, 1992; Martínez et al., 2001).

The 7–8 ka sediments were formed during the peak of the Holocene highstand, approximately during the peak of the global Climatic Optimum (Aguirre and Whatley, 1995), while younger Holocene terraces are thought to represent regressive sea-levels. During the Late Holocene the entire Argentine coast could have been tilted tectonically (Rostami et al., 2000).

3.2. Pleistocene deposits (MOIS5, MOIS7 and MOIS9?/11?)

Some of the Pleistocene deposits may be equivalent to the Pascua Fm. and Sangamon Interglacial sediments recognized in the Buenos Aires Province in northern Argentina, to the Chuy Fm. of Uruguay and to the Pleistocene transgression of ca. 123 ka documented for Brazil (Table 1).

The Pleistocene terraces IV and V are exposed in the south of Bahía Vera, from ca. 8 km NNW of Cabo Raso, in the north of Camarones, to ca. 12 km south of this small town (Fig. 1). They are composed of sand, gravel and shells, partially cemented by calcium carbonate, and covered by vegetation.

In the vicinity of Camarones, a fourth ridge system represents the oldest series of Pleistocene deposits (MTIII). These are typically exposed by a road-cut ca. 12 km NW of the city, and are mainly composed of pebbles cemented by calcium carbonate and scarce molluscs with weak taphonomic signatures, mostly the odd big *Ostrea* and other bivalve taxa generally highly abraded and encrusted with carbonate material.

The ages of the younger Pleistocene littoral terraces range between 92 and 250 ka. The oldest deposits, remnants of Middle Pleistocene beach ridge systems, are ca. 309–342 ka old. The dating available can be summarized as follows:

- MTV: The ages around 92 and 135 ka correlate with MOIS5 (probably when the sea level reached ca.+6 m above m.s.l., during times of warmer SST than present).
- MTIV: The age range of ca. 178–239 ka correlates with MOIS7, a highstand lower or similar with the present (or the same elevation as MOIS5e; Rostami et al., 2000) and a little colder than stages 1, 5, 9 and 11 (Ortlieb et al., 1996a,b).
- MTIII: The ages for this MT correlate with MOIS9 (a higher sea level, lower than MOIS5) but most probably with the longer MOIS11 (equal or higher than the present msl, longest and warmest of the last 500 ka; Winnograd et al., 1997; Zazo, 1999b). Based on the similarity of the molluscan content (especially *Ostrea* sp. and other bivalve species) these deposits could be correlated with the Belgranense sediments from the type locality in Buenos Aires Province (see below). On the other hand, Rostami et al. (2000) mentioned MOIS9 deposits in the area (+33–34 m above m.s.l.).

4. Modern littoral adjacent to the deposits studied

The modern littoral area was sampled, adjacent to the Quaternary terraces, from south of Bahía Vera and Bahía Camarones down to Caleta Sara (next to Cabo Dos Bahías). It is characterized by open marine conditions and oceanic climate, with cold-temperate waters (3–14.5 °C) of euhaline conditions (34–35‰) and gravelly–sandy substrates.

The area is influenced by the cool Malvinas (Falkland) Current which flows from the southernmost tip of the South Atlantic Ocean northwards to Golfo Nuevo in Chubut. It belongs to the Magellanean Zoogeographic Province, which extends between Golfo Nuevo and Tierra del Fuego. A contrasting current, the warm Brazilian Current, extends northwards from Golfo Nuevo to southern Brazil. Golfo Nuevo (ca. 43°S) determines the southernmost boundary of the Argentinean Zoogeographic Province.

Along the SW Atlantic the atmospheric circulation pattern is strongly influenced by the position of the Anticyclonic Centre which shifts seasonally. In turn, it controls the summer and winter shifts of the warm (Brazil) and cool (Malvinas) shallow oceanic currents and water masses (warm-temperate and cool-temperate, respectively). More detail on the modern area surrounding the fossiliferous deposits sampled can be obtained from Knox (1960) and Boltovskoy (1979).

5. Sites, samples, methods, problems

The fossil molluscan shells were collected in selected outcrops along the study area. The fossiliferous sites (Figs. 1 and 2) belong to MTIII (+44 m, Camarones), IV (+22–29 m, Punta Pescadero and Camarones) and V (+16–18 m, Bahía Vera, Punta Pescadero, Camarones) (Pleistocene) and MTVI

(+8–14 m, Punta Lobería, Punta Pescadero, Camarones) (Holocene) (Tables 1 and 2). This broad coastal zone was chosen to complete our records, as it represents a gap in our studies of molluscan assemblages from Quaternary marine sedimentary deposits along the Chubut Province. Of most importance, this area offers the opportunity to study very well preserved molluscan assemblages from raised beaches already well studied from geomorphological, sedimentological and chronostratigraphical points of view. The area is therefore essential for understanding biotic responses to climate change linked to sea-level oscillations with relatively precise chronological control.

Samples which consist of coarse sands, shell debris and pebbles were collected at 14 sites: ten fossiliferous (PA02Q10-16, 16bis; PA02Hol5-7) and four modern localities (PA02M4, 5, 7) (samples marked as Q, H, M in Fig. 1). Fossils were sampled atop the terraces, all the material is entirely from open-ocean habitats and was accumulated as storm deposits. Most are whole molluscan shells and only a few articulated bivalve shells can be found within a matrix of sand, coarse gravel and boulders. Bivalves preserved in growth position are scarce, while disarticulated shells dominate and belong to specimens mostly reworked from different nearby strata.

Bulk samples of fossil molluscs consisted of ca. 400 cm^3 (sediment and shells) collected at natural exposures, abandoned quarries, and well preserved outcrops or at road cuts. Of these eight are of Pleistocene and three of Holocene age: two belong to MTIII (PA02Q16, 16bis), four to MTIV (PA02Q10, 11, 13, 14), two to MTV (PA02Q12, 15), and three to MTVI (PA02Hol5, 6, 7). No samples have been dated in this study. Whenever possible shell samples of this study come from levels in terraces dated by previous authors (mainly Schellmann and Radtke, 2000; Rostami et al., 2000; other references in Table 2). These are marked with * in Fig. 2 (equivalent to samples PA02H6, PA02Q12, 15; PA02Q16). In Figs. 1 and 2 and Table 2 we refer to the cross-sections and stratigraphic columns illustrated by these authors and mention the ages available.

Empty shells from the modern littoral were collected in bulk samples from the supralittoral and intertidal zones along the area adjacent to the fossil beach deposits. Modern samples are PA02M4, 5, 5(o), 5’, and 7.

Quaternary molluscs are useful tools as indicators of environmental and climatic changes through time. Those from nearshore environments, a more unstable and complex scenario than the open ocean, must be carefully used as palaeoenvironmental signals regarding substrate, energy levels, and SST. However, previous attempts have yielded interesting results complementing geological studies (Ortlieb et al., 1996a,b; Murray-Wallace et al., 2000; Lutaenko et al., 2002; Aguirre, 2002, 2003).

The faunal composition of the four Quaternary marine terraces was examined and systematic, palaeoecologic and palaeobiogeographic aspects of the molluscs were reviewed and updated in terms of palaeoenvironmental reconstruction of the littoral area since at least MOIS9 or MOIS11.

Identification of the typical molluscs for at least the last four sea-level highstand episodes was based on the occurrence, relative abundance, species richness, and diversity indices (Margaleff’s, d, and Shannon–Weaver, H”) obtained for samples of the different MT (III–VI). Comparisons of assemblages between different MT, for which dating with modern techniques is available, in an area where modern conditions and fauna are known, allow correlations with MOIS and should also help to objectively distinguish them from the molluscan composition of pre-Quaternary Patagonian terraces and of the modern benthic communities.

Based on the global isotope curve (Haq et al., 1987; Zazo, 1999a,b; Winnograd et al., 1997) there is general agreement in assuming a SST higher than at present during MOIS5e (Last Interglacial maximum; ca. 125 ka BP) and MOIS1 (Mid-Holocene transgressive maximum, ca. 5–8 ka BP) and also that the MOIS5e highstand was the warmest since the Mid-Pleistocene. One problem still to be solved is that MOIS11 (ca. 423–362 ka BP; Zazo, 1999b) in South America could be the longest and warmest of the Pleistocene interglacial highstands preserved (Ortlieb et al., 1996a; Chilean coast). Earlier Burckle (1993) established that in the Southern Ocean Stage 11 was very warm and characterized by increase in calcium carbonate and proposed that was longer and warmer than the succeeding interglacials.

The area and deposits studied here around and south of Camarones (MTIII), which could be interpreted as MOIS11, could help to test whether MOIS11 was warmer than MOIS5e also at the eastern margin of southern South America. Another problem is to decipher based on a palaeobiogeographic approach whether our molluscs show biotic responses of the litttoral biota to climatic changes. Did all the species have the same distribution since the Mid-Pleistocene? Do shifts of their geographic boundaries reveal favourable (warm) or unfavourable (cold) climatic conditions? Extinction of taxa or shifts (expansions, retractions) in their geographic ranges for different time spans in comparison with the present are among the major effects of climate variability linked to the Quaternary glacial cycle dynamics.

An analysis of this kind for the Holocene, such as the one performed previously for other coastal areas in Argentina (Aguirre, 2001), is a good example for addressing the problem of the record of the Climatic Optimum in Patagonia and its palaeobiogeographic effect.

6. Faunal composition of the coastal deposits

6.1. General composition

The marine terraces contain molluscan skeletons (gastropods and bivalves) associated with occasional crustacean, cnidarian, bryozoan, terebratulid brachiopod, and polychaete remains. Molluscs represent 91% of the total fauna in assemblages from adjacent modern nearshore environments. In all, 41 taxa belonging to 25 genera were identified with gastropods (24 species) outnumbering bivalves (17 species) (Table 3).

Micromolluscs have not been identified and microfossils have so far not been recovered or mentioned in the local literature. Synchronous deposits studied southwards along Bahía Bustamante area contain several foraminifers and ostracods (Aguirre et al., in press). Therefore it is most likely that future, more exhaustive sampling will show their presence along the Camarones area as well.

6.2. Preservation

Most samples contain a majority of whole shells mixed with shell fragments and small pieces of rocks. The shells show variable modes of preservation. In general, shells are better preserved in younger (Holocene) deposits. The bivalve shells are generally oriented at random in most strata but they have also been found horizontally or, in very few cases, in growth position. Gastropods have most often been found as whole shells.

Shells of epifaunal taxa (bivalves and gastropods) most often are less well preserved (higher degree of fragmentation, abrasion, dissolution) than infaunal bivalves. The bivalve shells show a better preservation than most gastropods, with the exception of mytilids (*Mytilus* sp., *Aulacomya atra*), which in many cases were found broken or highly abraded.

An outstanding observation is that in nearly all the Pleistocene samples where *Tegula atra* occurs very commonly the shells have retained their original colour and nacreous layer, in spite of the age of the deposits (more than 90 ka, MTIV and MTV) and in spite of the epifaunal habit of this species, which exposed it more to transport within high energy environments. This species can be regarded as an autochthonous element of the assemblages from these MT.

6.3. Diversity of the molluscan assemblages

Qualitative and semi-quantitative estimations were performed to make the palaeoenvironmental interpretation more precise and informative. Differences in the relative abundance of the taxa and diversity indices were observed in samples from different terraces (Figs. 3 and 4).

Along the study area the most characteristic taxa recorded are the gastropods: *Nacella* (*P.*) *deaurata* (Gm.), *N.* (*P.*) *magellanica* (*Gm.*), *Fissurella* spp., *Crepidula protea* (d'Orb.), *C. dilatata* Lamk., *Natica isabelleana* d'Orb., *Buccinanops* spp. and *Trophon* spp., and the bivalves *B. purpuratus* (Lamk.), *P. antiqua* (King), *Clausinella gayi* Hupé, *Mactra* cf. *patagonica* d'Orb., and *Ostrea tehuelcha* Feruglio. In the modern littoral along Bahía Vera, Punta Pescadero, Cabo Raso, and Bahía Camarones, the most typical taxa are *A. atra*, *C. gayi*, *Aequipecten tehuelchus* and *P. antiqua* (bivalves), and *Crepidula* spp., *Trophon geversianus* and *Nacella* spp. (gastropods) (Fig. 5). Some taxa, which occur

Table 3
General biogenic composition of the beach ridge systems sampled

SPECIES GROUPS (I-IV)		AGE	PLEISTOCENE								HOLOC			MODERN					
		SAMPLES	PA02Q1	PA02Q11	PA02Q12	PA02Q13	PA02Q14	PA02Q15	PA02Q16	PA02Q16bis	PA02HOL5	PA02HOL6	PA02HOL7	LIVING off modern littoral	PA02M	PA02M	PA02M5´	PA02Mo	PA02M7
		MARINE TERRACE	IV	IV	V	V	IV	V	III	III	VI	VI	VI	R	R	R	R	R	R
		GASTROPODS																	
IV	1	*Fissurella picta* (Gm.)			X								X	X					
IV	2	*Fissurella oriens* Sowerby	X									X		X		X			
IV	3	*Fissurella radiosa* Lesson	X		X									X		X			
IV	4	*Nacella (P.) magellanica* (Gmelin)	X	X	X						X	X	X	X	X	X			X
IV	5	*Patinigera deaurata* (Gmelin)	X	X							X	X	X	X	X	X	X		X
IV	6	*N.(P.) delicatissima* (Strebel)												X	X	X	X		X
III	7	*Tegula patagonica* (d' Orbigny)						X				X		X	X	X	X		
IV	8	*Tegula (C.) atra* (Lesson)	X		X			X					X	NO					
I	9	*Crepidula aculeata* (Gmelin)											X	X	X	X			
III	10	*Crepidula onyx* Sowerby		X										X	X	X			
III	11	*Crepidula* cf. *unguiformis* (Lamarck)												X		X			
III	12	*Crepidula protea* d' Orbigny	X	X	X			X				X	X	X	X	X	X		
I	13	*Crepidula dilatata* Lamarck	X	X	X			X			X	X	X	X	X	X			
III	14	*Natica isabelleana* d' Orbigny		X										X					
III	15	*Trochita pileus* (Lamarck)												X		X			
III	16	*Trophon varians* (d' Orbigny)		X	X			X			X	X	X	X	X		X		
III	17	*Trophon geversianus* (Pallas)		X						X	X	X		X	X	X	X		X
III	18	*Odontocymbiola magellanica* (Gmelin)	X	X										X		X			
	19	*Volutidae indet.*									X		X	X					
III	20	*Buccinanops globulosus* (Kiener)	X	X	X			X					X	X	X	X			
III	21	*Buccinanops* sp.							X	X				X					
IV	22	*Acanthina monodon* (Pallas)						X						X					
IV	23	*Pareuthria plumbea* (Philippi)			X							X	X	X					
III	24	*Siphonaria lessoni* (Blainville)						X						X			X		X

SP GROUP		BIVALVES	PLEISTOCENE								HOLOC			MODERN					
			PA02Q10	PA02Q11	PA02Q12	PA02Q13	PA02Q14	PA02Q15	PA02Q16	PA02Q16bis	PA02HOL5	PA02HOL6	PA02HOL7	LIVING off modern littoral	PA02M4	PA02M	PA02M5´	PA02Mo	PA02M
		MARINE TERRACE	IV	IV	V	V	IV	V	III	III	VI	VI	VI	R	R	R	R	R	R
I	1	*Mytilus (M.) edulis* (Linné)			X			X				X	X	X					
II	2	*Brachidontes (B.) rodriguezi* (d' Orb.)			X								X	?		X		X	X
IV	3	*Brachidontes (B.) purpuratus* (Lamk.)	X	X	X			X				X	X	X		X	X		X
IV	4	*Brachidontes* cf. purpuratus (Lamk.)			X								X	X	X				
IV	5	*Aulacomya atra* (Molina)		X							X		X	X	X	X	X	X	
III	6	*Aequipecten tehuelchus* (d' Orbigny)	X							X		X	X	X	X	X		X	
IV	7	*Chlamys patagonicus* King												X		X			
	8	Pectinidae indet.							X	X				X					
II	9	*Ostrea tehuelcha Feruglio*							X	X				NO					
III	10	*Mactra* cf. *patagonica* d' Orbigny							X	X				X					
IV	11	*Eurhomalea exalbida* (Dilwyn)												X		X			

Table 3 (*continued*)

SP GROUP		BIVALVES	PLEISTOCENE								HOLOC			MODERN					
			PA02Q10	PA02Q11	PA02Q12	PA02Q13	PA02Q14	PA02Q15	PA02Q16	PA02Q16bis	PA02HOL5	PA02HOL6	PA02HOL7	LIVING off modern littoral	PA02M4	PA02M	PA02M5´	PA02Mo	PA02M
		MARINE TERRACE	IV	IV	V	V	IV	V	III	III	VI	VI	VI	R	R	R	R	R	R
III	12	*Protothaca antiqua* (King)	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	
III	13	*Clausinella gayi* Hupé	X	X				X						X	X	X		X	
III	14	*Veneroida* indet.					X	X						X					
III	15	*Pitar rostratus* (Koch)					X	X		X				X		X			
IV	16	*Panopea abbreviata* Valenc.												X		X			
III	17	*Lyonsia* sp.												X					X
		Other Invertebrates																	
		Balanus sp.	X	X	X							X	X	X		X			
		Terebratulid brachiopods							X	X				X		X	X	X	
		Bryozoa								X				X					
		Corals								X				X					

OUTCROPS (PA02H, PA02Q):

PA02Hol (Holocene)
PA02Hol5: Punta Pescadero
PA02Hol6: Cabo Raso
PA02Hol7: Camarones

PA02Q (Pleistocene)
PA02Q10: S Bahía Vera
PA02Q11: S Bahía Vera
PA02Q12: Punta Pescadero-Cabo Raso
PA02Q13: N Camarones (Cabo Raso)
PA02Q14: N Camarones (Cd. *M. isabelleana* ?)
PA02Q15: N Camarones (MTIV ?)
PA16: NW Camarones (MTIII)
PA16bis: NW Camarones (MTIII)

MODERN LITTORAL (PA02M): adjacent Magellanean Province

PA02M4= Punta Pescadero
PA02M5= S Bahía Vera
PA02M5´= S Caleta Raso
PA02Mo= S Bahía Vera-Punta Lobería
PA02M7= Caleta Sara

Additional information can be obtained from sampling for previous studies along the Patagonian coasts (Aguirre, 2003; Aguirre et al., in press) and from the local literature cited.

R= recent

along the modern shore adjacent to the fossiliferous sites, i.e., *Chlamys patagonicus*, *Fissurella picta*, *Nacella delicatissima*, *Crepidula* cf. *unguiformis*, and Volutidae indet., have not been recorded in the marine terraces (Table 4).

New records in this area for the Late Pleistocene MTIV and V (MOIS7 and MOIS5) are *Crepidula aculeata*, *C. onyx*, *C. protea*, *N. isabelleana*, *Brachidontes rodriguezi*, *A. tehuelchus*, and *C. gayi*, and for the Holocene (MTVI, MOIS1) *Fissurella oriens*, *F. radiosa*, *Nacella deaurata*, *Tegula patagonica*, *C. protea*, *N. isabelleana*, *Trophon varians*, and *B. rodriguezi*.

Within the oldest Pleistocene terrace, Pectinidae indet., *Ostrea* cf. *tehuelcha* and *Mactra* cf. *patagonica*, together with other taxa recorded by Feruglio (1950) (i.e., *Corbula patagonica*, *Diplodonta vilardeboana*), are characteristic for the MTIII (MOIS11/9?; ca. 350–400 ka BP). Typical of the MTIV (MOIS7, ca. 225 ka BP) are *T. atra*, big *P. antiqua*, and Veneroida indet. The assemblage of the MTV (MOIS5, 125 ka ?) contains typically *T. atra*, *T. patagonica*, *Crepidula dilatata*, *Mytilus edulis*, *B. purpuratus*, *P. antiqua, Pitar rostratus*).

Within the Holocene, MTVI (ca. 6.7 ka BP) is characterized by *B. purpuratus*, *N.* (*Patinigera*) *magellanica*, *N.* (*P.*) *deaurata*, *T. geversianus*, *B. purpuratus*, and *A. atra*.

Exclusive for the modern littoral are *Chlamys* sp., *Panopea abbreviata*, *Lyonsia* sp., and *N. delicatissima* (Figs. 3–5).

Apart from qualitative compositional differences, an outstanding observation is the dominance and greatest size of *T. atra* and of *P. antiqua* in the Pleistocene (especially within MTIV) and of *Trophon* spp., *A. atra, B. purpuratus* in the Holocene (MTVI) or along the modern littoral area.

Species richness (*Margaleff́s Species Richness*, *D*) (Fig. 4): As expected, the modern samples (PA02M4, M5, M5́, M5o, M7) and the Holocene sites (H5, H6, H7) exhibit the highest species values as they represent more complete populations (less taphonomic loss is expected to occur in samples of younger age). A modern sample from south of Bahía Vera (M5, Fig. 1) shows the highest richness. Among the fossil samples, the highest richness belongs to the Holocene samples (PA02Hol7, MTVI). The lowest richness values were observed in the Pleistocene terraces, especially in samples from MTV (PA02Q14) and MTIII (PA02Q16, 16bis, Table 3).

Diversity indices (*Margaleff index*, *d; Shannon–Weaver index*, *H″*) (Fig. 4) are in general agreement with the species richness values. As expected, the Margaleff index is highest in the modern samples, especially those from southern Bahía Vera-Punta Lobería (PA02M5, M5o), followed by the Holocene MTVI (PA02Hol7) while the minimum values belong to the Pleistocene (PA02Q15, MTV), except for sample PA02Q11 (MTIV), which reaches the maximum value for the Holocene. Similar results were obtained with the Shannon–Weaver index. The highest diversity belongs to modern samples (PA02M4 and M5), followed by samples PA02Hol7 and PA02Q11.

Overall, these results agree with similar results obtained from coeval marine terraces southwards of the area of study, along the coastal area of Bahía Bustamante–Caleta Malaspina, where the highest species richness and diversity indices among the fossil samples were observed in deposits dated at ca. 6–7 ka, and coincide with the peak of the Holocene transgression.

In summary, diversity is in general terms lower in older (Pleistocene MOIS11, 7, 5) than in the younger (Holocene) deposits of the area of study, but most probably is related to SST conditions. Our present data reinforce previous interpretations suggesting that the controlling factor for the increase in biodiversity must have been climate instead of time as proposed by other authors (Leighton, 2001).

Moreover, the Holocene assemblages from the Camarones area appear richer and more diverse than those along the surrounding terraces at Bahía Bustamante area and southwards along Golfo San Jorge. Conversely, they are less diverse than similar coeval beach deposits preserved northwards along the shoreline of the Buenos Aires Province. This pattern suggests a latitudinal gradient in taxonomic diversity, but whether this could have been caused by a spread of taxa from low- to high-latitude, due to the older age of the tropical oceans in comparison with the polar oceans (Crame, 2000), is not known. As expected, the southwards decreasing trend of molluscan diversity is in accordance with decreasing SST at higher latitudes.

The Pleistocene terraces in this area contain more diverse faunas than the surrounding Patagonian terraces and the restricted Pleistocene outcrops and sites known from the Bonaerensian coastal area. This situation may be the result of abrasion and reworking after deposition of the Belgranense or Pascua Bonaerensean sediments (Table 1) by the subsequent Holocene transgression, reducing the preservation potential of the original assemblages.

7. Palaeoecology

Data on the ecological requirements of modern representatives for each species are summarized on Table 4. All the taxa are benthic euhaline inhabitants of different oceans, mostly of the shelves of the South Atlantic Ocean. The majority of these species live in the intertidal and/or upper infralittoral zones, although the most abundant ones are found in the supralittoral and intertidal. As a whole, they are indicative of high energy conditions and hard substrates (coarse sand and pebbles or rocky bottoms) (Fig. 6a).

Bivalves are excellent palaeoecological indicators and infaunal taxa offer more precise palaeoenvironmental information than epifaunal species. By contrast, gastropods offer less reliable information, as most of the species recovered are epifaunal and more exposed to transport prior to their final burial

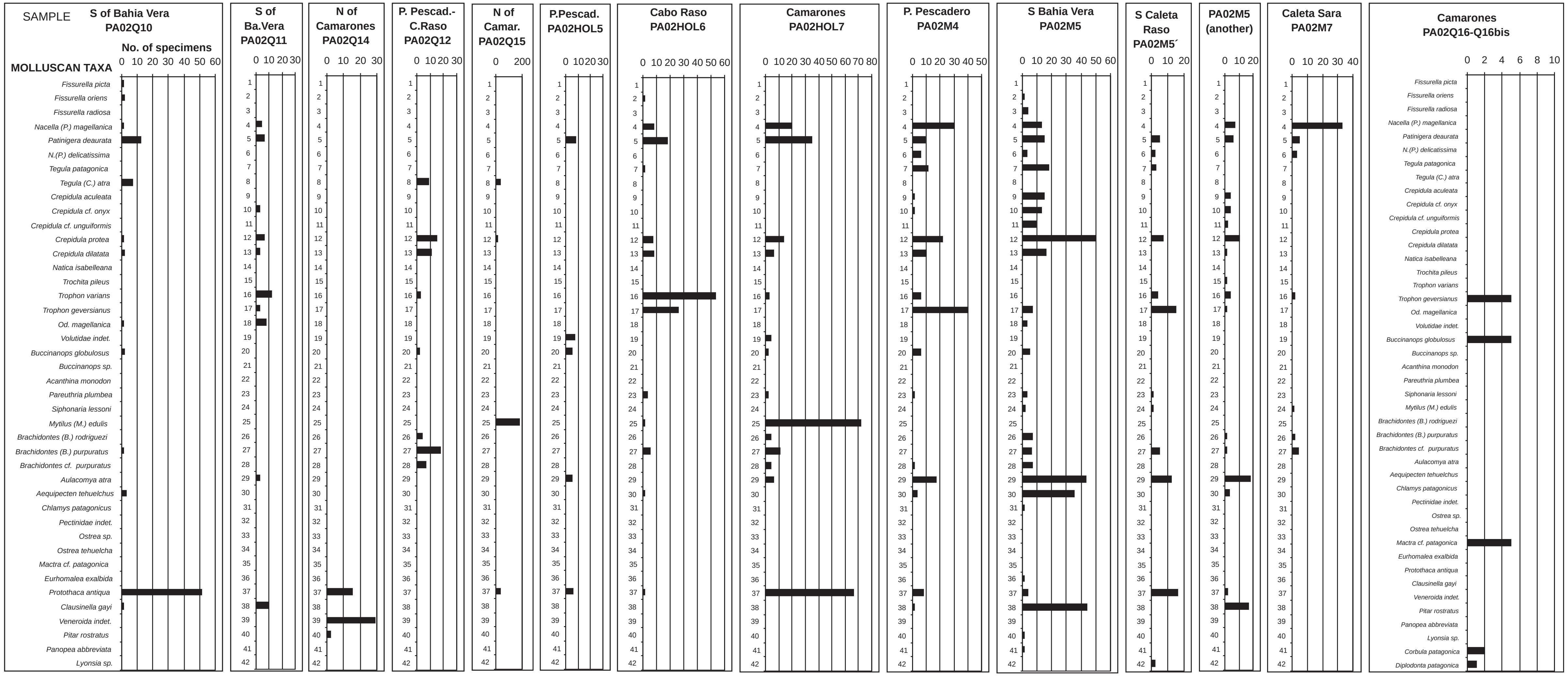


Fig. 3. Faunal composition and relative abundances of the most characteristic molluscan taxa of the marine terraces studied (M: modern; Hol: Holocene; Q: Pleistocene). Note that sample Q13 is not illustrated (no fossils recovered) and sample Q14 contains no gastropods.

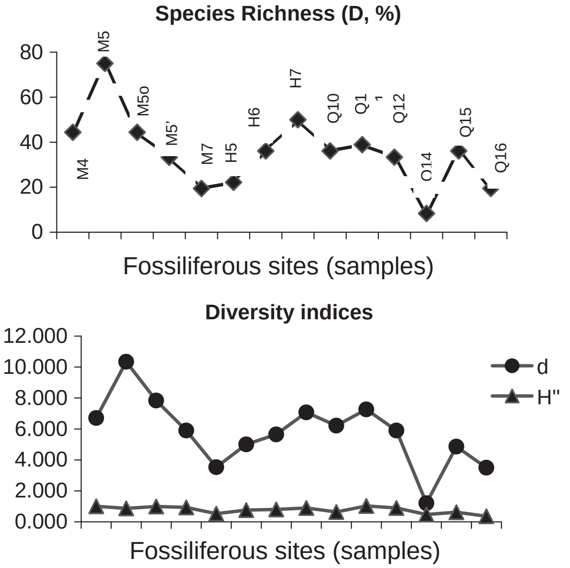


Fig. 4. Species richness (*D*, %), Margaleff diversity index (*d*) and Shannon–Weaver diversity index (*H*″).

in beach deposits, but they can provide useful data about depth, bottom and energy conditions of the original environment.

8. Geographic and stratigraphic distribution

All the species recovered have living representatives, mostly in the Antillean, Brazilian, Argentinean and Magellanean zoogeographic provinces (Fig. 1). At present most of these taxa are found nearshore adjacent to the MT, mainly in cool-temperate or typically cold water masses. One exception is *O. tehuelcha* Feruglio, an extinct warm water species which has only been recorded within sediments of MTIII. Another interesting observation is that *T. atra* (Lesson), a cold water species characteristic for the Pleistocene MTIV and MTV, at present lives in the Pacific Ocean from Peru to Estrecho de Magellanes (Figs. 6b, and 7), but is absent on the Atlantic side of South America where it has only fossil records along Chubut and Santa Cruz provinces. No other bivalve became extinct after deposition of MTIII (since MOIS11), nor any gastropod after deposition of MTIV and V (since at least MOIS7).

No dramatic migrations or shifts in the geographic ranges of the taxa have been observed, except for *T. patagonica*, *N. isabelleana* and *B. rodriguezi*, which show at present a northwards migration along the SW Atlantic (Argentinean Province), and *T. atra*, which is not represented at the Atlantic margin of South America as mentioned above. Both cases are probably biotic responses (alternating expansions and retractions) to climate changes occurred during interglacial episodes. These palaeobiogeographic responses took place during the Holocene and Pleistocene highstands correlated with MOIS1 and MOIS5-7, respectively.

The palaeobiogeographic analysis shows that, as a whole, the molluscan fauna has a temperate or cool-temperate character. According to their modern distribution our taxa can be classified into four groups, typical of constrained shallow water masses and marine zoogeographic provinces: I, pandemic; II, Antillean; III, Argentinean; IV, Magellanean (Aguirre, 1993, 2003). Variations in percentages of these groups are useful tools for speculations on SST conditions and climate variability in nearshore environments since the Mid-Pleistocene (Fig. 8).

Most taxa from the Pleistocene terraces at Bahía Vera–Bahía Camarones and those from the Holocene ridges are identical. Among the total molluscan taxa identified, 34% range back to the Miocene, 34% range from the Pleistocene to present, and 12% range from the Holocene to present. *O. tehuelcha* occurs exclusively in the Pleistocene, and *T. atra* dominates in the Pleistocene. 15% of the taxa exclusively occur in the modern littoral.

9. Comparisons with other Quaternary coastal deposits from Argentina

Several species preserved in the Quaternary of the study area also occur in other Pleistocene and Holocene deposits of Argentina (Zanjón El Pinter Fm., Caleta Malaspina Fm.; San Antonio Fm., Baliza San Matías Fm., Las Escobas Fm., Mar Chiquita Fm.) (Table 1).

Most species recorded at Bahía Vera–Bahía Camarones occur southwards in Patagonia, in the MTIV, V and VI along the Bahía Bustamante–Caleta Malaspina coastal area (Zanjón El Pinter Fm., Caleta Malaspina Fm.) and along Golfo San Jorge (MTV and VI). The affinities with assemblages from coeval ridges exposed northwards in the Río Negro Province (San

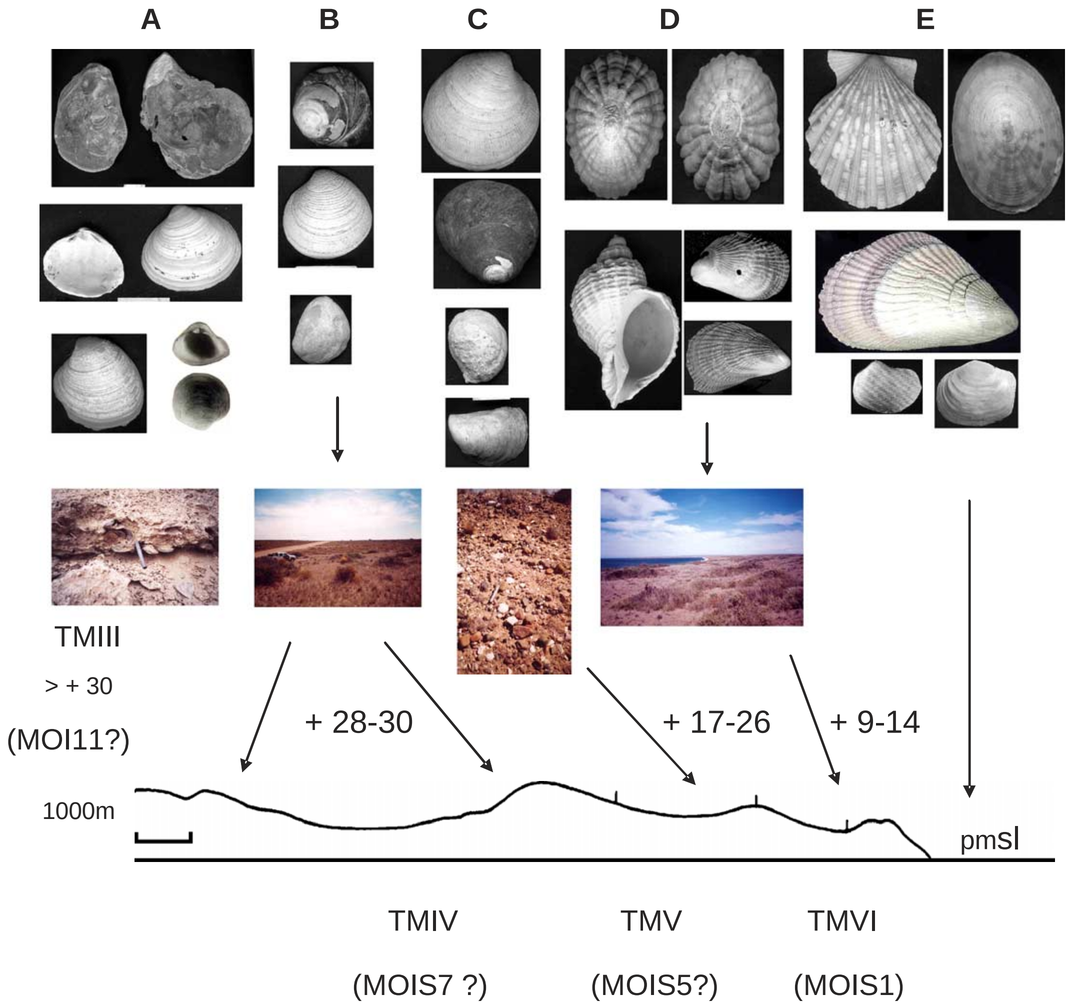


Fig. 5. Most characteristic molluscan taxa of the marine terraces and of the modern littoral in the Bahía Vera–Camarones area. Cross-section modified from Feruglio (1950, p. 89) at Bahía Camarones area. Altitude taken from the literature and MOIS of previous authors, based on ESR, Th/U or D/L ages of samples from equivalent units (Feruglio, 1950; Schellmann and Radtke, 2000, Rostami et al., 2000). A (MTIII, is not in this section, samples taken from exposures southwards of Camarones): *Ostrea* cf. *tehuelcha* (H=113)*, Mactra* aff. *isabelleana* (L=37)*, Pitar rostratus* (L=30), *Corbula patagonica* (L=11), *Diplodonta vilardeboana* (L=14); B (MTIV): *Tegula atra* (W_m=23*, Protothaca antiqua* (L=55)*, Clausinella gayi* (L=28)*, Crepidula protea* (H_m=11.8); C (MTV): *Tegula atra* (W_m=25) (maximum size), *Protothaca antiqua* (L=49), *Crepidula dilatata* (H_m=19), *Mytilus edulis* (L=48); D (MTVI): *Nacella deaurata* (W_m=35)*, Nacella magellanica* (W_m=37), *Trophon geversianus* (H_m=49)*, Brachidontes purpuratus* (L=18), *Aulacomya atra* (L=72); E (modern): *Aequipecten tehuelchus* (H_m=47)*, Nacella delicatissima* (W_m=29), *Aulacomya atra* (L=72), **Lyonsia* sp. (L=16), **Panopea abbreviata* (L=35) (*not collected, but mentioned in the literature). Dimensions in mm. L=length, H=height; W_m=maximum width; H_m=maximum height.

Antonio Fm., Baliza San Matías Fm.) are less strong. In comparison with molluscan assemblages sampled northwards of the study area, along the Bonaerensean area in deposits of the Las Escobas Fm. (Samborombon Bay), Mar Chiquita Fm. (Mar Chiquita–Mar del Plata area) and around Bahía Blanca, the taxa which are absent from the study area are more abundant (see Appendix).

In Tierra del Fuego (Gordillo, 1991, 1998) only some of the cold water species are common (*M. edulis, B. purpuratus, Protothac antiqua, Mulinia edulis, Eurhomalea exalbida, Mactra sp.; Nacella* *magallanica, N. deaurata, Fissurella spp., T. atra*) and the assemblages are characterized by comparatively lower species richness (ca. 19%).

The molluscan assemblages from MTI and II in nearby Patagonian localities contain a totally different molluscan fauna (Feruglio, 1936–1937), including taxa which are absent from the marine Quaternary of central Patagonia, which probably formed during the Pliocene highstands. Several taxa recorded in the Quaternary of Patagonia have been recorded in deposits of the Miocene transgression (Del Río and Martínez, 1998; Aguirre and Farinati, 1999) (Table 4).

10. Palaeoenvironmental interpretations

Comparisons of fossil and living littoral molluscs from the area of study suggest that Pleistocene and Holocene environments must have been roughly similar to the modern nearshore in terms of substrate, salinity, and depth. The palaeoecological analysis of individual bivalve and gastropod taxa and their geographic ranges support that they are indicative of hard substrates, shallow waters and fully marine conditions, similar to the modern intertidal and upper infralittoral zones along the SW Atlantic in central Patagonia.

Faunal differences between the Pleistocene, Mid-Holocene and present (Magellanean Province) show biotic responses to climate changes during glacial cycles and suggest that, most probably, changes of SST mainly controlled the observed differences through time. Secondarily, slight local variations in substrate conditions or water energy must have also influenced the littoral biota.

The abundance of patelliform gastropods and mytilids within the Holocene terrace (MTVI) suggests a relatively harder substrate and shallower conditions in comparison with the previous Pleistocene highstands. *Nacella* (*P.*) *magellanica*, *N. (P.) deaurata*, *T. geversianus*, *B. purpuratus*, and *A. atra* are indicative of the existence of an extensive rocky shore and of patches of sandy infralittoral and intertidal areas in which the fossil assemblages lived.

Differences in diversity and relative abundance, both latitudinally and chronologically, are linked to environmental controls, mainly to temperature conditions. Maximum taxonomic richness and highest diversity are generally expected at low latitudes and in warm waters, where generally greater percentages of tropical, subtropical or warm temperate species are found. This pattern has been accepted unequivocally for epifaunal taxa, while it is rather controversial for infaunal taxa. However, a latitudinal diversity gradient closely related with SST has been shown in other shelf areas for the total marine benthos (infaunal and epifaunal taxa) (Roy et al., 2000).

The molluscan data show that diversity was highest in sample PA02Hol7 (ca. 6–7 ka, Table 2), which coincides with the peak of the Holocene Climatic Optimum. This could imply that the biodiversity was driven by climate control, not by time, as observed in similar assemblages of MT along Bahía Bustamante.

Within the Pleistocene terraces, the lowest diversity corresponds to a sample from MTIV (36.11 in sample PA02Q14, MOIS7), while for the remaining Pleistocene (i.e., PA02Q10, 11, MTIV; PA02Q12, 15, MTV) and Holocene samples (PA02Hol5, 6) the values are roughly similar (Fig. 4). Regarding the assemblages identified in the oldest terrace (MTIII), the species richness (*D*) is relatively low (17.7), probably as a result of the high degree of cementation and fragmentation of the shells preserved, which causes considerable taxonomic primary loss.

Changes in temperature (SST) along this area are evidenced by variations in composition, size variability and, mainly, by geographic shifts of the molluscan taxa, although not as drastic as documented for other coastal zones (California, Pacific, Peru, Chile; Valentine, 1958, 1994; Campbell and Valentine, 1977; Rollins et al., 1987; De Vries and Wells, 1990; Ortlieb et al., 1995, 1996a,b; Roy et al., 1995, 2000; Sandweiss et al., 1998; Maasch et al., 2001).

In general terms, in the study area gastropods seem to have been more sensitive than bivalves to SST variations linked to sea-level highstands (Figs. 4 and 7). A greater abundance of elements, which occur at present in temperate to warm-temperate masses (Group III), and lower quantities of other taxa typical of cold waters (Group IV) characterized the Mid-Holocene transgression (Fig. 8).

For the Pleistocene MTIV and V there is no clear evidence of higher SST in comparison with the Holo-

Table 4
Ecological requirements and distribution in time and space of characteristic taxa

Palaeoecological data	Range									Depth			SUBSTRATE		MODE OF LIFE			
	Stratigraphic				Geographic													
Bivalves	M	PL	HOL	REC	PAND	ANT	BRAZ	ARG	MAG	Supral.	Intert	Sublit	Soft	Hard	Epibys	Cement	Sh.inf	Deep in
Mytilus edulis	X	X	X	X	X						X	X		X	X			
Brachidontes purpuratus	X	X	X	X					X	X	X	X		X	X			
Brachidontes rodriguezi	X	X	X	X			X	X	X	X	X	X		X	X			
Aulacomya atra		X	X	X			X	X	X		X	X		X	X			
Aequipecten tehuelchus	X	X	X	X			X	X				X	X	X	X			
Chlamys patagonicus				X				X	X			X	X		X			
Pectinidae				X								X						
*Ostrea*sp.	X	X	X	X		X	X	X	X			X		X		X		
Ostrea tehuelcha			X									X		X		X		
Mactra patagonica		X	X	X			X	X				X	X				X	
Eurhomalea exhalbida		X	X	X				X	X		X	X	X				X	
Protothaca antiqua	X	X	X	X			X	X	X			X	X				X	
Clausinella gayi			X	X			X	X	X			X	X				X	
Pitar rostratus		X	X	X			X	X	X			X	X				X	
Panopea abbreviata				X														
Lyonsia sp.		X	X	X			X	X	X			X	X				X	
Gastropods	M	PL	HOL	REC	PAND	ANT	BRAZ	ARG	MAG	Supral.	Intert.	Sublit.	Soft	Hard	F S	Carniv	Herb	Filtr
Fissurella picta				X						X	X	X		X			X	
Fissurella oriens		X		X					X	X	X	X		X	X		X	
Fissurella radiosa		X	X	X				X	X	X	X	X		X	X		X	
Nacella(*P.*)*magellanica*			X	X				X	X		X	X		X	X		X	
N(*P.*)*deaurata*		X	X	X				X	X	X	X	X		X	X		X	
N(*P.*)*delicatissima*				X					X	X	X	X		X	X		X	

Tegula patagonica	X	X	X	X				X			X	X		X	X		X	
Tegula (*C.*) *atra*		X		X				X	X		X	X		X	X		X	
Crepidula aculeata				X	X	X	X	X	X		X	X		X				X
Crepidula cf. *onyx*		X	X	X							X	X		X	X			X
Crepidula cf. *unguiformis*				X							X	X		X	X			
Crepidula protea	X	X	X	X		X	X	X			X	X		X	X			X
Crepidula dilatata	X	X	X	X	X	X	X	X	X			X		X	X			X
Natica isabelleana	X	X	X	X			X	X	?			X	X					
Trochita pileus			X	X					X		X	X	X		X		X	
Trophon varians	X	X	X					X			X	X	X	X	X	X		
Trophon geversianus	X	X	X	X				X	X		X	X		X	X	X		
Pareuthria plumbea		X	X	X				X	X		X	X		X	X	X		
Odontocymbiola magellanica		X	X	X				X	X		X		X		X	X		
Volutidae indet.				X								X	X		X	X		
Buccinanops globulosus		X	X					X	X		X	X	X		X	X		
Buccinanops paytensis		X	X	X					X		X	X	X		X	X		
Buccinanops sp.		X	X	X			X	X	X		X	X	X			X		
Acanthina monodon			X	X					X			X	X	X		X		
Pareuthria plumbea			X	X					X		X	X	X	X		X		
Epitonium sp.	X		X	X				X			X	X	X		X		X	
Ataxocerithium pullum		X	X	X					X		X		X	X	X		X	
Siphonaria lessoni			X	X	X		X	X	X	X	X	X		X	X		?	

Stratigraphic range: M: Miocene, PL: Pleistocene, HOL: Holocene, REC: Recent. Geographic range: PAND: pandemic, ANT: Antillean Province, BRAZ: Brazilian, ARG: Argentinean, MAG: Magellanean. Depth: Supral.: supralittoral zone; Intert.: intertidal; Sublit.: sublittoral. Mode of life: Epibys.: epibyssate; Cement.: cemented; Sh.inf.: shallow infaunal; Deep in: deep infaunal. F: free living; S: sessile; Carniv.: carnivorous, Herb.: herbivorous, Filtr: filter feeding.

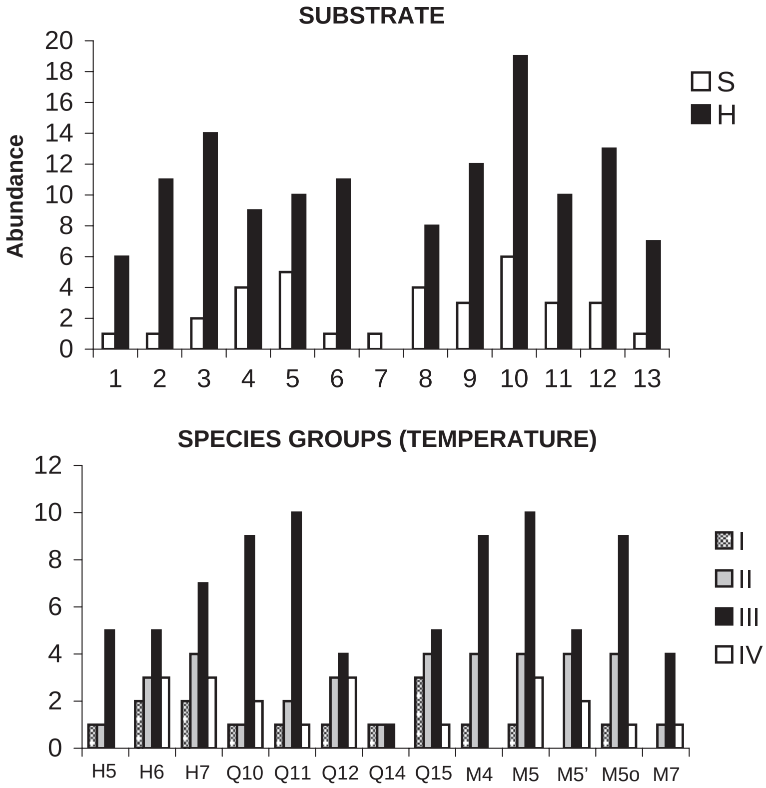


Fig. 6. Substrate and SST preferences of the taxa present in the samples. 6a, Substrate preferences of the most characteristic taxa: S = soft, H = hard; 6b, Distribution of species groups (I–IV, according to their distribution in shallow water masses) fossil and modern samples. 1–3: Holocene samples (PA02Hol5–7); 4–8: Pleistocene samples (PA02Q10–15); 9–10: modern samples (PA02M4, 5, 5́, 5o, 7).

cene. Cold water (Group IV) gastropods were more abundant, while bivalves were slightly scarcer. However, both gastropods and bivalves of group IV were less abundant in these terraces than at present in the Magellanean Province. On the contrary, dominance of species assigned to group III in the Pleistocene MTIII suggests that it was deposited during higher SST in comparison with the present and the Mid-Holocene (Fig. 8).

Shape variation of individual taxa, such as intraspecific morphological differences in *Patinigera*, *Crepidula*, *Tegula*, and *Brachidontes*, can be correlated with substrate conditions, depth, and energy conditions of the littoral area. Other observations point to differences in size and abundance between fossil vs. modern assemblages:

- The higher abundance of shells of *Nacella* spp. in the Holocene than in the Pleistocene is probably related to their preference of coarser substrate. The greater size of modern shells than that of shells from the Quaternary terraces probably reflects their cold water affinity and a decrease in SST since MOIS1.
- The big size of *T. patagonica* characterizes the Holocene MTVI; the occurrence of this species is indicative of warm temperate waters typical of the Argentinean Province.
- The greater size of *T. atra*, a species typical of cold waters of the Magellanean Province, in Pleistocene MTIV and V than in the Holocene MTVI, is related to the higher SST of the Mid-Holocene.
- The bigger size of *Crepidula* spp. is typical of Holocene and modern nearshore areas, where coarse sandy and rocky bottoms predominate.
- Comparatively large *B. rodriguezi* are found at present in warmer waters northwards along the Argentinean Province, while the shells are smaller

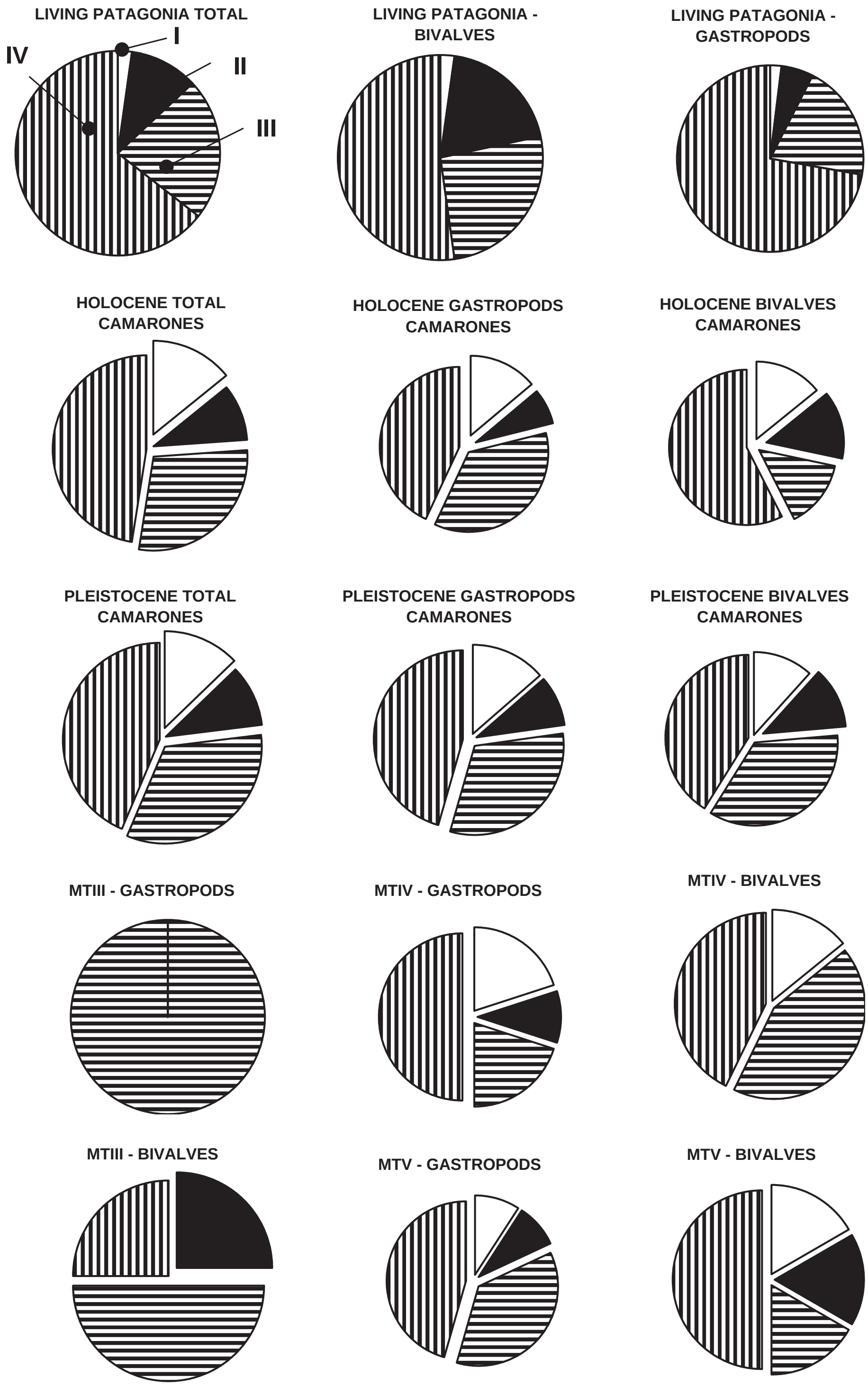
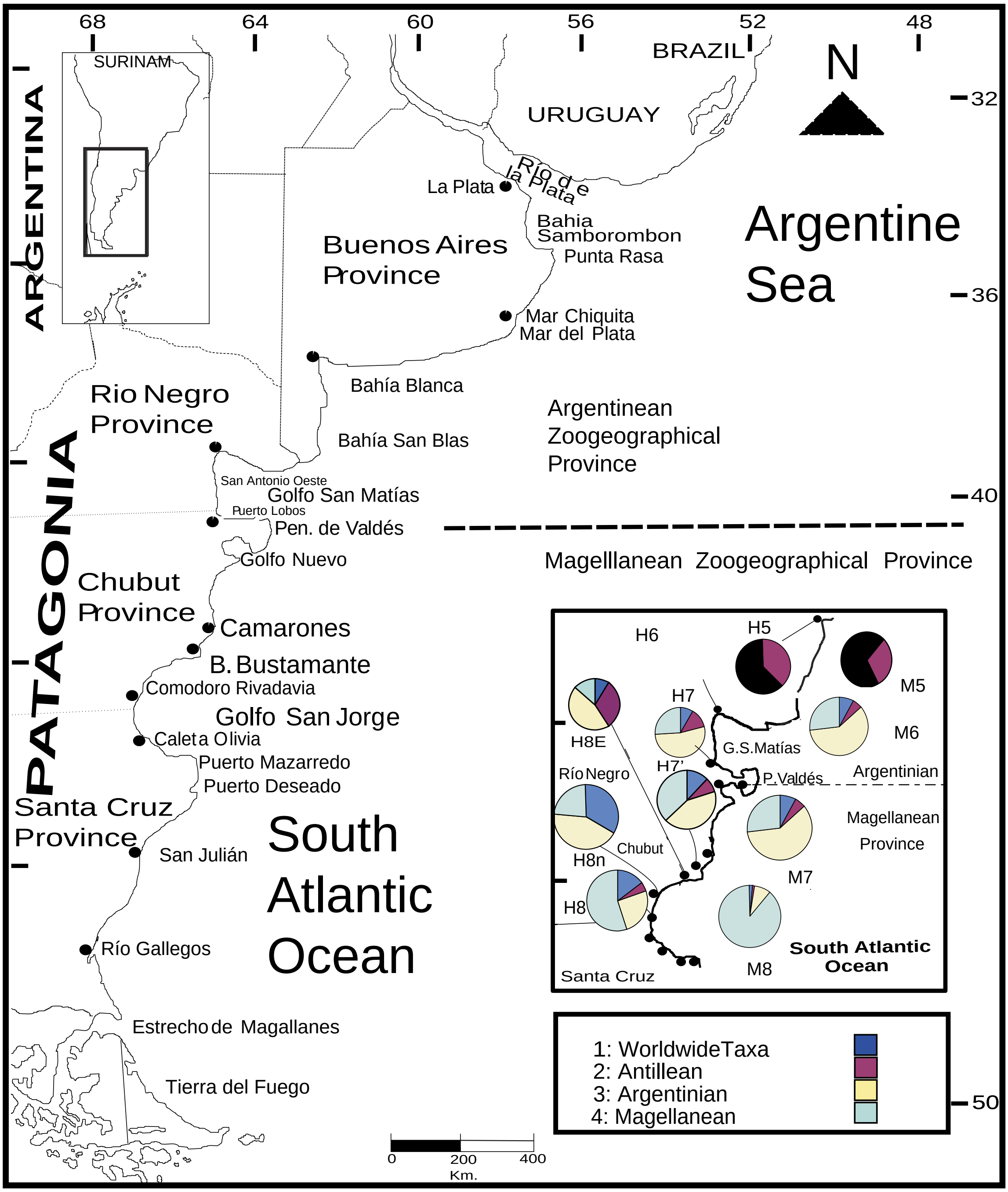


Fig. 7. Relative abundance of species grouped according to their distribution in water masses of constrained SST (I–IV). Comparison between the present, Mid-Holocene (MTVI) and Pleistocene (MTV, IV and III) (Bahía Vera–Camarones area and Patagonia in general).

and scarce in the Pleistocene MT and along the adjacent nearshore. By contrast, greater percentages of *B. purpuratus*, fossil and living, indicate cool SST in the study area.

- The modern littoral is characterized by big shells of *Chlamys* sp., *P. abbreviata*, *N. delicatissima*, and *Lyonsia* sp. and by higher abundances of taxa typical of cold waters (Carcelles, 1950; Castellanos



and Landoni, 1988–1993; Bastida et al., 1992; Roux et al., 1995; Forcelli, 2000).

11. Discussion

Levels of extinctions, migrations and quantitative compositional variations of typically warm or cold water taxa as well as changes of diversity patterns through time generally accompany sea-level fluctuations and changes in SST. These biotic responses are primary effects of climate changes governing biogeographic dynamics of Quaternary glacial cycles.

However, although it is possible to establish molluscan records characteristic of former coastlines and comparisons between Pleistocene interglacials and the Mid-Holocene transgression, a precise linkage with highstands of the last 400 ka in this area and with consequent shifts in oceanic and atmospheric circulation patterns due to climate change is not yet available.

It is difficult to measure the amount of variation in temperature per unit of time. There is still no precise evidence about the MOIS preserved as MTVI, V, IV and III. Further modern dating of selected molluscs need to be compared with the stable isotopic composition (δ^{18}O and δ^{13}C) of the same taxa. Stable isotope variations should offer a more precise pattern of environmental variations through time. Only since the Mid-Holocene (ca. 8 ka) it is possible to provide more precise data on palaeoclimate changes. No such evidence is as yet accurately documented for the Pleistocene MTV and IV, which could belong to highstands of MOIS5 (5e, 5a ?, 5c?) and MOIS 7, or for MTIII (MOIS9/11?) in central Patagonia according to dating by previous authors.

Based on our present knowledge of the molluscan assemblages studied (qualitative, quantitative, morphological and distributional variations), a comparison with modern associations (Carcelles, 1950; Bastida et al., 1992; Castellanos and Landoni, 1988-1993]) on a temperature basis suggests slightly higher than present SST during the Mid-Holocene (MTVI, MOIS1, Hypsithermal), slightly lower temperature for MTV (MOIS5c ?), similar for MTIV (MOIS5e ?, 7?) and higher temperatures for MTIII (MOIS11 ?).

11.1. Holocene climatic optimum

The effect of the Holocene Climatic Optimum on the littoral molluscs of central and southern Patagonia is still open to debate. In fact, Holocene deposits in Argentina have provided contradictory conclusions regarding the occurrence of the Climatic Optimum (Bonaerensian littoral) (Aguirre, 1993) or its absence (Patagonia) (molluscs, microfossils) (Pastorino, 2000; Boltovskoy, 1979). A recent review (Aguirre, 2001) suggested higher SST than at present following a southwards decreasing trend of warm water species and latitudinal displacements during the Mid-Holocene: A greater percentage of warm (35%) and a small percentage (6%) of cold taxa ca. 7.5–4.5 ka ago (Bonaerensian area) and a higher percentage (47%) of warm-temperate and cold taxa (33%) ca. 9–6 Ka ago (Patagonia) in comparison with the present suggest a

Fig. 8. Relative abundances of species (groups I–IV defined according to their occurrence in warm water masses of different SST) in the study area, and modern boundary of the Argentinian and Magellanean zoogeographic provinces. Mid-Holocene (H) vs. modern (M) relative abundances of species groups according to their preferences for shallow water masses, along the study area and in adjacent coastal areas (for the Buenos Aires Province quantities are shown for group II and in black the remaining elements altogether). M5: Puerto Quequén (SEBuenos Aires Province), M6: G.S.Matías (Río Negro Province), M7: P.Pirámides (Chubut Province), M8: Chubut and Santa Cruz provinces. H5: Bahía Blanca (Buenos Aires Province), H6: S.A.Oeste (Río Negro Province), H7: P.Pirámides (Chubut), H7′: Camarones (Chubut), H8E: B. Bustamante (Chubut); H8n: B. Solano (Chubut); H8: C. Rivadavia (Chubut). Both modern (M) and Holocene (H) localities show a southward trend in the abundance of groups I–IV. Holocene percentages relate to the age and latitudinal position of the deposits. During the Mid-Holocene high sea-level stand, groups II and III were higher than at present. In Patagonia, the southwards decreasing trend of groups II and III (higher at 8–5 ka, loc. 24=H7′ and decreasing after ca. 4 Ka at loc. 27=H8, Post-Hypsithermal) is accompanied by an increase of group IV, which was still scarcer than at present (for example H5–H8 vs. M5–M8). Ages according to uncorrected radiocarbon dates available for the area and deposits analysed (see references in Tables 1 and 2 and Aguirre, 2002).

southwards displaced Mid-Holocene palaeo-oceanographic pattern (warm Brazilian and cool Malvinas currents).

During the Mid-Holocene, in comparison with the present and with previous Pleistocene highstands, there was a greater proportion in the study area of species now living in the Argentine Province or northwards (Groups III, II) than of taxa typical or exclusive of cold water masses (IV). The ecological preferences of the taxa and the scarcity or absence of other typically cold taxa common today in the Magellanean Province at the same latitude suggest that the original communities lived in a similar shallow environment. But at the time of deposition of the MTVI (ca. 6–7 ka BP) the SST was somewhat higher than at present (Fig. 8), most probably during the Mid-Holocene global Climatic Optimum ("Hypsithermal").

For example, sample PA02Hol7 not only exhibits the highest diversity, but nearly 50% of the species (i.e., *C. protea*, *Trochita pileus*, *T. varians*, *B. globulosus*, *B. rodriguezi*, *A. tehuelchus*) range typically from southern Brazil to Río Negro, indicating a minimum SST of ca. 18°C (warm temperate water mass, sensu Knox, 1960). In general terms, gastropods seem to be more sensitive than bivalves to SST variations linked to sea-level highstands (Figs. 6b and 7) (higher abundance of elements which occur at present in temperate to warm-temperate masses (III) and the lower quantities of typically cold water taxa (IV) (Fig. 8).

This palaeobiogeographic response of the nearshore biota to the effect of the Hypsithermal was proposed on molluscan evidence for the coastal area between the Río de La Plata and Bahía Blanca, Bahía Bustamante, and Golfo San Jorge. Our present data reinforce this hypothesis, although only slight variations characterized this event in central Patagonia. During the Holocene Optimum the sea occupied much of Patagonian coastal area as the global warming coincided with the transgressive maximum (ca.+6 m above m.s.l.). Within this scenario the mean annual temperature possibly was 1–2 °C higher than at present.

Our Mid-Holocene assemblages can be correlated with the Holocene Optimum in other zones dated at 7500/6500–5000 B.P. (Australia, South Africa, Japan, Kurile Islands, Korea) confirming that this event was global in extent (Aguirre, 1993, 2001; Avery, 1993; Lutaenko, 1993; Cohen and Tyson, 1995; Lutaenko et al., 2002; Razjigaeva et al., 2002). However, in the studied areas along Patagonia, such as Bahía Vera-Camarones, Bahía Bustamante–Península Gravina, and Golfo San Jorge, migration of biogeographic zones are not apparent. The evidence obtained in this study reflects only that, due to the climate warming, the Brazilian Current was intensified and the Malvinas (Falkland) Current exerted less influence than at present (Aguirre et al., in press).

A fluctuating rainfall pattern at about the time of deposition of the shells during the Hypsithermal was hypothesized for beach ridges of the Las Escobas and Mar Chiquita formations and in the Bahía Blanca area along Buenos Aires Province (Aguirre et al., 2002; González et al., 1983). It was hypothesized that during the Hypsithermal the warmer climate caused a southwards shift of the South Atlantic Anticyclonic Centre, responsible for seasonal rainfall over that area. This shift was accompanied by a similar displacement of the warm-temperate shallow water masses and of the zoogeographic boundaries. A similar pattern could also have been existed along Patagonia, which should be documented by variations in the isotope composition of molluscan shells. These series of events were also witnessed in the SW African Holocene (Cohen and Tyson, 1995) and may account to some degree for an hemispheral trend.

11.2. Pleistocene highstands

Palaeoclimatic changes that occurred since the Mid-Pleistocene are recognized worldwide as global in extent. The warmest peaks are placed during MOIS1 (Holocene) and, even stronger, during MOIS5e (Last Interglacial), both times of higher than present sea-level stands (Haq et al., 1987; Zazo, 1999b; Kukla et al., 2002). Slightly lower highstands and SST are thought to have characterized MOIS7 and 11. However, MOIS11 is the highest and warmest in the Pacific margin of South America (Ortlieb et al., 1996a, Chilean coast).

In the study area there is no such evidence for the Pleistocene MTIV and V of higher SST in comparison with the Holocene interglacial. Cold water gastropods (Group IV) were more abundant, while bivalves were slightly scarcer. However, both gastropods and bivalves of group IV were less abundant in these terraces than they are at present in the Magellanean Province. The composition and the diversity values in MTIV and MTV suggest cool temperate rather than warmer SST for MOIS7 and 5. On the contrary, a dominance of species assigned to group III suggests that the Pleistocene MTIII (MOIS11 ?) there was deposited during higher SST in comparison with the present and with the Mid-Holocene (Fig. 7).

The MTV (PA02Q12, 15), equivalent to samples dated by Schellmann and Radtke (2000) at 92–115 ka (MOIS5c ?) and 117–135 ka (MOIS5e ?), was proposed to indicate the Last Interglacial (Table 2). The assemblage (*T. atra*, *T. patagonica*, *C. dilatata*, *M. edulis*, *B. purpuratus*, *P. antiqua*, *P. rostratus*) is not indicative of a climatic optimum like the Last Interglacial maximum highstand (MOIS5e) as recorded worldwide (Muhs et al., 2002; Kukla et al., 2002). Most probably, the molluscan shells of MTV lived during MOIS5a or c (not MOIS5e). According to Schellmann and Radtke (2000) there is no precise knowledge based on ESR dating on whether the ages assigned to MOIS5 can be accurately considered MOI5a, 5c or 5e. The ecology of the molluscs confirms an original environment not indicative of warmer waters during MOIS5e. On the contrary, the assemblage is indicative of cold SST similar to modern conditions at the same latitude, in agreement with the original interpretation by Feruglio (1950).

In the MTIV (MOIS7?, ca. 178–220 ka BP) *T. atra*, the maximum size of *P. antiqua*, and the low diversity suggest lower SST than during the Holocene interglacial.

In contrast, the assemblage of MTIII (MOIS11?; ca. 350–400 ka BP), consisting mostly of enormous *O. tehuelcha* d'Orbigny, extinct in the adjacent littoral, suggests warmer SST. Although slightly lower highstands and SST are thought to have characterized MOIS7 and 11 globally, the hypothesis of MOIS11 being the highest and warmest in South America (Ortlieb et al., 1996a,b) seems to be confirmed by our data for the Atlantic margin, if the ages are correct (Table 2).

Another aspect regarding MTIII is its correlation with the Pleistocene beach deposits preserved northwards along the Bonaerensian coastal area. Curiously, the shells of *O. tehuelcha* are very similar to the oysters from the type locality of the 1 stage (Pleistocene) preserved very locally in Buenos Aires Province. Traditionally, the Belgranense deposits were interpreted as the Last Interglacial highstand (and correlated with the Pascua Fm.) (Table 1) but have recently been documented as a pre-Last Interglacial highstand on magnetostratigraphic evidence (Nabel, 2002). This interpretation is in accordance with the faunal content and taphonomic attributes of our material, which reveal more similarity with older faunas (Miocene).

Our present data reinforce many general palaeoenvironmental interpretations by Feruglio (1950) and can be integrated with the whole molluscan records and bibliographic data gathered for a more extensive Patagonian coastal area, along Chubut and Santa Cruz provinces (Bahía Vera–Golfo San Jorge).

11.3. Comparison with other coastal areas during the Late Quaternary

Quaternary marine molluscs have been studied in several areas of South America, such as along the Atlantic margin at Surinam, southern Brazil, and Uruguay (Altena, 1969, 1975; Closs and Forti, 1971; Sprechmann, 1978; Martínez et al., 2001). Along the Pacific coast, most studies focused on Peru and Chile (Ortlieb and Díaz, 1991; Ortlieb et al., 1995; Perrier et al., 1994; Guzmán et al., 1995, 1998; De Vries et al., 1997; Sandweiss et al., 1998; Maasch et al., 2001).

The main conclusion regarding the general composition of the molluscan assemblages preserved along both margins of South America, either in marine terraces and beach deposits or in coastal lagoonal facies, is that at the species level a low similarity is apparent. However, the dominant taxa at both sides share similar or identical ecological requirements, and can be considered palaeoecologically equivalent components of the littoral biota.

The molluscan fauna preserved in beach ridges of Surinam (Altena, 1969, 1975), at the Atlantic coast of northern South America, exhibits a very low similarity with the Patagonian assemblages. As expected, the diversity is higher at these low latitudes. Only a few genera are common with the assemblages studied here or with other coastal deposits along Patagonia: *Glycymeris*, *Chlamys*, *Ostrea*, *Mactra, Mulinia*, *Pitar*, *Protothaca*, *Corbula*, *Lyonsia* (Bivalves); *Fissurella*, *Diodora*, *Epitonium*, *Littoridina*. In most cases they differ at the species level, although they are palaeoecologically equivalent.

The Quaternary molluscan assemblages of Brazil (Forti, 1969; Closs and Forti, 1971) share the following genera: *Glycymeris*, *Brachidontes*, *Chlamys*, *Ostrea*, *Pitar*, *Protothaca*, *Clausinella*, *Mactra*, *Corbula* (Bivalvia); and *Littoridina*, *Tegula*, *Epitonium*, *Crepidula*, *Natica*, *Olivancillaria*, *Olivella*, *Buccinanops*, and *Adelomelon* (Gastropoda).

The genera in common with Quaternary marine ridges from Uruguay (Sprechmann, 1978; Langguth, 1980) are the bivalves: *Glycymeris*, *Mytilus*, *Brachidontes*, *Chlamys*, *Ostrea*, *Mactra*, *Pitar*, and *Corbula* and the gastropods *Diodora*, *Tegula*, *Littoridina*, *Crepidula*, *Epitonium*, *Olivella*, and *Buccinanops*.

In Peru and Chile the molluscs of Quaternary ridges and terraces show strong taxonomic differences. Overall, the common genera are mainly *Protothaca*, *Aequipecten*, *Aulacomya*, *Mytilus*, *Brachidontes* (Bivalvia) and *Fissurella*, *Tegual* and *Siphonaria* (Gastropoda).

These compositional differences observed for the Quaternary at both sides of South America probably are related to the origin and biogeographic history of the molluscan faunas. The dominant taxa of the Atlantic margin must have suffered dispersion from low tropical and subtropical latitudes (Antillean and Brazilian Provinces) towards the south (down to central Patagonia). This biogeographic process could explain the decreasing diversity in the same direction (from north to south) and must have occurred since the Late Miocene, with fluctuations during succeeding glacial cycles, causing expansions and retractions of the faunas and of their biogeographic boundaries according to changes in SST through time and in the intensity of the warm dominant currents. Whether this interpretation is correct, needs to be tested by biogeographical studies (endemicity, cladistic biogeography and panbiogeographic approaches) of the modern and Quaternary faunas (work in progress).

The molluscan assemblages of southern Patagonia, which show more common taxa with the Pacific terraces (i.e., *T. atra*, *Fissurella* spp., *Siphonaria lessoni*, *M. edulis*, *B. purpuratus*, *A. atra*, *M. edulis chilensis*) could be a result of the Pacific origin of the cold Magellanean fauna. These assemblages must have resulted from the mixing of two ancestral groups, a more recent Pacific group which mixed with the fauna dominating in the Atlantic, probably through dispersion along the Chilean coast by the cool current system. Similar interpretations based on different sources of evidence were presented elsewhere (López Gappa, 2000; Martínez and Del Río, 2002).

12. Conclusions

Molluscan assemblages preserved in coastal deposits along Bahía Vera–Bahía-Camarones (Chubut Province, central Patagonia) were assigned to four main marine terraces, MTIII (Camarones, higher than +30 m after Feruglio, 1950, older than 300 ka and probably ca. 400 ka; Rostami et al., 2000; Schellmann and Radtke, 2000), MTIV (Punta Pescadero and Camarones,+22–29 m, 178–239 ka), MTV (Bahía Vera, Punta Pescadero, Camarones,+16–18 m, 92–135 ka), and MTVI (Punta Lobería, Punta Pescadero, Camarones,+6–12 m, 2.5–8 ka). They provide useful preliminary results for palaeoenvironmental and palaeoclimatic interpretations of sea-level highstands since the Mid-Pleistocene.

1. The mollusc assemblages (91%; 24 gastropod, 17 bivalve species) collected at 14 localities (Pleistocene, Holocene, and modern sites) show latitudinal and temporal variations in composition, distribution, diversity patterns and morphology of individual taxa.
2. Approximately 34% of this fauna range back to the Miocene, 34% have records since the Pleistocene, 12% since the Holocene, and 15% exclusively occur in the modern littoral. *T.*

atra and *O. tehuelcha*, dominant in and exclusive of the Pleistocene, respectively, have no living representatives in the SW Atlantic Ocean.

3. The most relevant taxonomic differences with the northern coastal areas of the Río Negro and Buenos Aires provinces are due to the occurrence of *Littoridina australis* (d'Orb.), *Calliostoma* spp., *Urosalpinx* spp., *Adelomelon brasiliana* (Lamk.), *Zidona dufresnei* (Donovan), *Olivancillaria* spp., *Olivella* spp., (Gastropoda) and *Noetia bisulcata* (Lamk.), *Glycymeris longior* Sow., *Amiantis purpuratus* (Lamak.), *Raeta plicatella* (Lamk.), *Tagelus plebeius* Lightf., *Corbula lyoni* Pilsbry, and *Chama* sp. (bivalves).
4. Since the Mid-Pleistocene nearshore environments were characterized by hard substrates, and high energy and euhaline waters, similar to the modern littoral of central Patagonia in the SW Atlantic (Magellanean Province).
5. The variations between the faunas of the Late Pleistocene (MTIII, IV, V), Mid-Holocene (MTVI) and present (Magellanean Province), are a result of environmental conditions, of which SST of the shallow water masses was the main controlling factor.
6. New records for the Late Pleistocene in the area are *C. aculeata* (Gm.), *C. onyx* Sow., *C. protea* d'Orb., *T. patagonica* (d'Orb.), *N. isabelleana* (d'Orb.), *B. rodriguezi* (d'Orb.), *A. tehuelchus* (d'Orb.), and *C. gayi* (Hupé). For the Holocene, the taxa *F. oriens* Sow., *F. radiosa* Less., *Patinigera deaurata* (Gm.), *T. varians* (d'Orb.), and *B. rodriguezi* (d'Orb.) have been recorded for the first time. An extinction is shown by *O. tehuelcha* d́Orb., and migrations by *T. atra* (Lesson), *N. isabelleana* (d'Orb.), *B. rodriguezi* (d'Orb.), *C. patagonica* (d'Orb.), and *D. vilardeboana* (d'Orb.).
7. *Naticadelicatissima* (Strebel). *Chlamys* sp., *P. abbreviata*, and *Lyonsia* sp. characterize the modern nearshore. MTVI (MOIS1) is characterized by *B.* cf. *purpuratus*, *N. (Patinigera) magellanica* (Gm.), *N.(P.) deaurata* (Gm.), *T. geversianus* (Pallas), *B. purpuratus*, and *A. atra* (Molina). MTV (MOIS5c?, 5e?), characterized by *T. atra*, *T. patagonica*, *C. dilatata* Lamk., *M. edulis* Linn., *B. purpuratus*, *P. antiqua*, and *P. rostratus* (Koch), is not indicative of a climatic optimum such as the Last Interglacial maximum highstand (MOIS5e). Typical of MTIV (MOIS7) are *T. atra*, the biggest *P. antiqua* (King), and Veneroida indet., indicative of water temperatures similar to the present cold waters. Exclusively in MTIII (MOIS11) occur Pectinidae, *O. tehuelcha,* and *Mactra* cf. *patagonica* d'Orb. They, together with other taxa (i.e., *C. patagonica*, *D. vilardeboana*), suggest warmer SST than at present.
8. The MTIII assemblage (MOIS11?, ca. 400 ka BP) indicates warmer conditions than that of MOIS5e along this stretch of coast of eastern South America, in agreement with a previous hypothesis for the Chilean coast (Ortlieb et al., 1996a). The assemblage from this terrace could be correlated with the Belgranense deposits of the Bonaerensian littoral.
9. The Holocene Climatic Optimum (5–8 ka) is confirmed to have influenced the littoral biota in this area. A slightly higher SST (1–2°C) implied atmospheric and palaeoceanographic changes, with a southwards shift of the dominant warm (Brazilian) and cool (Malvinas = Falkland) currents along the SWAtlantic and, consequently, of the Argentinean and Magellanean marine zoogeographic provinces.
10. Extinctions, displacements and changes of relative abundances of stenothermic taxa reflect biotic responses of the molluscan faunas to sea-level oscillations and related environmental changes and fluctuations through time of palaeobiogeographic boundaries in response to climate variability. Future studies need to improve palaeoceanographic and palaeoclimatic reconstructions, which will help to solve the problem of the origin of the molluscan faunas from the SW Atlantic.
11. For the marine Quaternary of Argentina additional modern dating and stable isotope analyses performed on the same reliable taxa are needed. This is imperative to decipher with more precision biotic responses, linked to highstands correlated with MOIS of the global isotope curve.

Acknowledgements

We are grateful to Prof. J.O. Codignotto and R. Kokot for their help in the field and to E. Fucks, Luc Ortlieb, E. Schnack, and R. Violante for comments or discussions on several ideas discussed. Special thanks are due to Prof. F. Fürsich. We also thank Prof. U. Radtke and the editors. This study was partially supported by grant from FCNYM, UNLP (Incentivos N353), Agencia de Promoción Científica (PICT 07-10967) and Conicet, (PIP2005). This is contribution to IGCP437 and IGCP495.

Appendix A. Main molluscan compositional differences of other Quaternary coastal deposits of Argentina studied previously (Aguirre et al., in press) with the marine terraces along the area of this study (see Table 3) (* stands for taxa extinct in the adjacent littoral; source of information in Aguirre and Farinati, 2000; Aguirre, 2001; Codignotto and Aguirre, 1993)

	Bonaerensian area	Río Negro area	Ba. Bustamante–Ca.Malaspina area	Golfo S. Jorge area
Gastropod Taxa				
Lucapinella henseli (Martens)	■			
Colisella ceciliana d'Orb.			■	
Ataxocerithium pullum (Philippi)			■	
Calliostoma coppingeri (Smith)	■			
Calliostoma carcellesi Clench and Ag.	■			
Calliostoma nordenskjoldi Strebel	■			
Littoridina australis d'Orb.*	■	■		
Epitonium tenuistriatum (d'Orb.)	■			
Urosalpinx rushi Pilsbry*	■			
Urosalpinx cala Pilsbry	■			
Anachis avara (Say)*	■			
Ximenopsis muriciformis (King and Brod.)			■	
Morula necocheana (Pilsbry)	■			
Zidona dufresnei (Donovan)	■	■		
Adelomelon beckii (Broderip)				■
Adelomelon brasiliana (Lamk.)	■	■		
Olivella tehuelcha (Duclos)	■	■		
Olivancillaria urceus Roding)	■	■		
Olivancillaria uretai Klappenbach	■			
Marginella martini Petit	■			
Terebra gemmulata Kiener	■			
Dorsanum moniliferum (Val.)	■			
Buccinanops paytensis (Kiener)			■	
Turbonilla uruguayensis Pilsbry	■			
Puncturella conica (d'Orb.)	■			
Bivalve Taxa				
Nucula nucleus (Linn.)	■			
Nucula oblicua (Lamk.)	■			
Nuculana whitensis Farinati	■			
Adrana electa (Adams)	■			
Noetia bisulcata (Lamk.)*	■			
Glycymeris longior Sow.	■	■		
Musculus viator (d'Orb.)	■			
Plicatula gibbosa Lamk.	■			
Ostrea equestris Say	■	■		
Crassostrea rhizophorae (Guilding)*	■			
Diplodonta patagonica (d'Orb.)	■			

Appendix A (*continued*)

	Bonaerensian area	Río Negro area	Ba. Bustamante–Ca.Malaspina area	Golfo S. Jorge area
Bivalve Taxa				
Phlyctiderma semiaspera (Philippi)	■			
Carditamera guppyi Dall	■			
Mulinia edulis (King and Broderip)	■			■
Raeta plicatella (Lamk.)	■			
Darina solenoides (King)	■	■	■	
Solen tehuelchus d'Orb.		■		■
Macoma uruguayensis (Smith)	■			
Tellina petitiana d'Orb.	■			
Strigilla carnaria (Linn.)	■			
Semele proficua (Pulteney)	■			
Abra aequalis (Say)	■			
Tagelus plebeius (Lightf.)	■			
Donax hanleyanus Philippi	■			
Amiantis purpuratus (Lamk.)	■			
Tivella isabelleana (d́ Orb.)	■			
Anomalocardia brasiliana (Gm.)*	■			
Petricola lapicida Chemn.	■			
Petricola pholadiformis Lamk.	■			
Petricola patagonica d'Orb.				■
Venericardia procera (Gould)				■
Sphenia hatcheri Pilsbry	■			
Corbula lyoni Pilsbry	■			
Hiatella arctica (Linn.)				■
Cyrtopleura lanceolada (d'Orb.)	■			
Barnea lamellosa (d'Orb.)	■			
Nettastomella darwin (Sow.)	■			
Lyonsia alvarezii	■			
Entodesma patagonicum (d'Orb.)	■			
Periploma ovatum d'Orb.	■			
Thracia similis Couthouy	■			
Bushia rushi (Pilsbry)	■			

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