

Holocene molluscan assemblages in the Magellan region*

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SUMMARY: In the Magellan region, much of the shoreline of the Beagle Channel coast (54°53'S; 67° - 68°W) is bordered by Holocene raised beaches, which contain a large number of molluscs and other shelled taxa. The purpose of this work is to document the presence of various molluscan assemblages deposited with little or no *postmortem* transportation. An epifaunal *Chlamys patagonica* palaeocommunity (ca. 8,000 - 7,000 BP) and three infaunal (*Tawera gayi*, *Ameghinomya antiqua* - *Hiatella solida* and *Ameghinomya antiqua* - *Ensis macha*) palaeocommunities (ca. 4,400 - 4,000 BP) were recognized. All the assemblages studied represent shallow, subtidal, cold-temperate environments. Based on comparisons with modern benthic communities in this region, these associations show that no remarkable ecologic and climatic changes occurred during the period ca. 8,000 - 4,000 BP. Thus, an apparent stability of modern marine communities over a period of several thousand years is suggested.

Key words: Holocene, molluscan assemblages, Magellan region.

RESUMEN: ASOCIACIONES DE MOLUSCOS DEL HOLOCENO EN LA REGIÓN DE MAGALLANES. En la región de Magallanes, gran parte de la costa del Canal del Beagle (54°53'S; 67°-68°O) está caracterizada por la presencia de playas elevadas del Holoceno, que contienen un gran número de moluscos y otros taxones. El objetivo de este trabajo es documentar la presencia de distintos tipos de asociaciones de moluscos depositadas sin previo transporte o escaso transporte *postmortem*. Se reconocieron una paleocomunidad epifaunal de *Chlamys patagonica* (ca. 8.000 - 7.000 AP) y tres paleocomunidades infaunales de *Tawera gayi*, *Ameghinomya antiqua*-*Hiatella solida* y *Ameghinomya antiqua*-*Ensis macha* (ca. 4.400 - 4.000 AP). Todas estas asociaciones representan ambientes marinos costeros templado-fríos. Al comparar las asociaciones estudiadas con las unidades equivalentes actuales no se han detectado cambios ecológicos y climáticos durante el período considerado ca. 8.000 - 4.000 AP, lo que sugiere un período de estabilidad de las comunidades de moluscos de varios miles de años.

Palabras clave: Holoceno, asociaciones de moluscos, región de Magallanes.

INTRODUCTION

Holocene marine molluscs are widely preserved in the geological record. Nevertheless, the majority of these fossil molluscan assemblages -closely associated with the offshore to beach gradient- consist of preburially transported assemblages

(allochthonous assemblages), which have little palaeoecological interest. This is not the case of the mollusc assemblages considered in this work, which have two characteristics used as tools for palaeoecological interpretations: (1) they were deposited *in situ* (autochthonous assemblages), or with little preburial transport (parautochthonous assemblages), and (2) the species are living taxa in the Magellan region. As used here, the term "sub-

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fossil" refers to animal remains of Holocene age, *i.e.* up to 10,000 years old.

The purpose of this work is to document the systematics of the subfossil species, the taphonomic evidence and the mollusc assemblage types. In addition, the trophic relationships and the ecological and palaeoecological characteristics of the species are discussed.

The Beagle Channel (54°53'S, 67°-68°W) is located in the Magellan region within the Fuegian Andes environment. Late Jurassic volcanic rocks (Lemaire Fm.; Borello, 1969) follow the potential Paleozoic-early Mesozoic basement (Lapataia Fm.; Borello, 1969). Cretaceous marine rocks overlay this formation (Yahgan Fm.; Kranck, 1932). Eocene continental beds (Slogget Fm.; Caminos, 1980) intruded by eruptive rocks (Quartino *et al.*, 1989) represent the Tertiary. The stratigraphical scheme is

completed with Quaternary sediments: Pleistocene glacial deposits and Holocene marine terraces. Holocene raised beaches border much of the shoreline of the Beagle Channel coast. During the Holocene, the palaeogeographic evolution of the Beagle Channel terraces system has been mainly controlled by glacioisostatic uplift and partly by neotectonic activity, notably by displacements on several minor faults (Rabassa *et al.*, 1989; Gordillo *et al.*, 1992).

According to Iturraspe *et al.*, (1989) the Beagle Channel shows an average temperature at 2 m depth of 6.5°C, with a maximum of 10°C (February) and a minimum of 3°C (August); and salinity varies from 27 to 31‰.

The localities considered in this work (Fig. 1) were selected on the basis of the features of the molluscan assemblages previously studied by

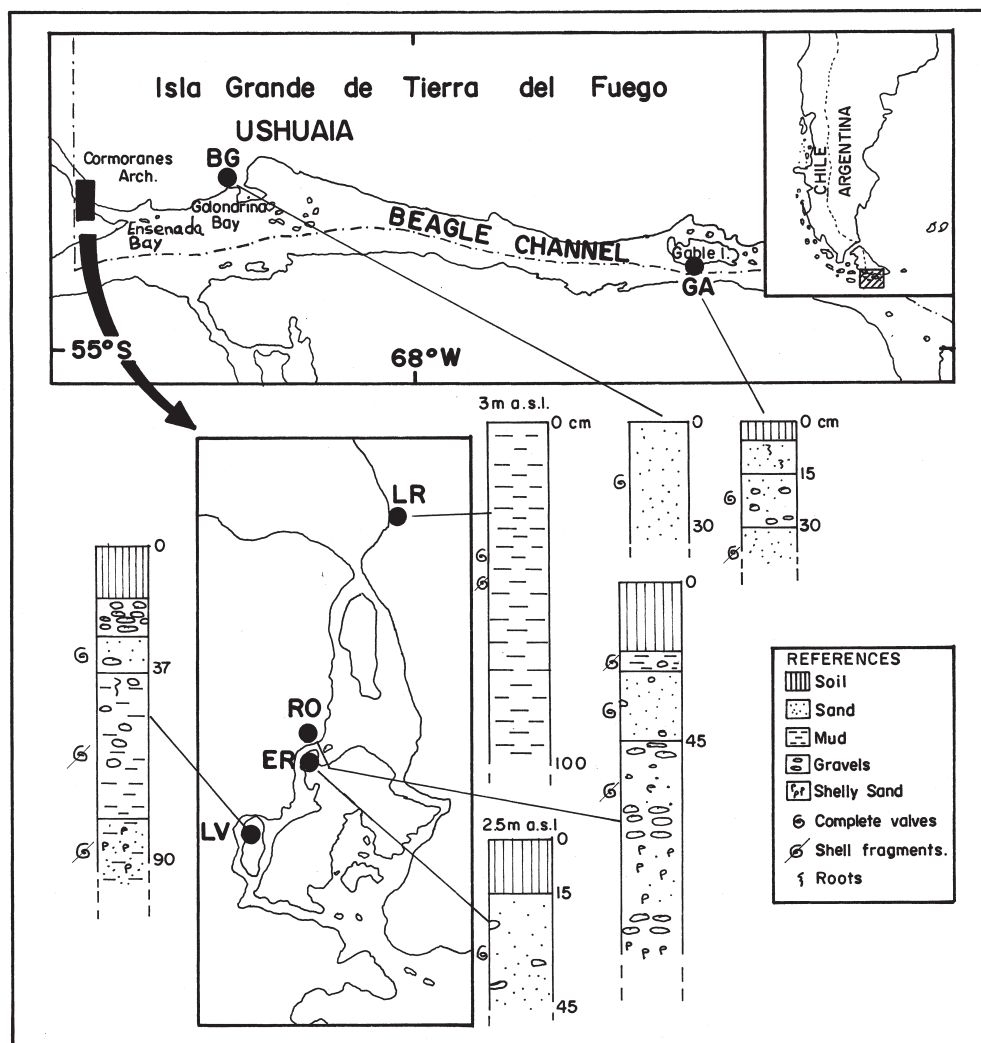


FIG. 1. – Map of the Beagle Channel showing sampling locations. LR: Lago Roca; RO: Río Ovando; ER: Entre Ríos; LV: Laguna Verde; BG: Bahía Golondrina and GA: Isla Gable.

Gordillo (1993) and Gordillo *et al.* (1993). In the western sector, Figure 1 shows the Cormoran Archipelago which includes the Lago Roca (LR), Río Ovando (RO), Entre Ríos (ER) and Laguna Verde (LV) sites. Low islands where Holocene deposits contain molluscs buried in situ cap this area. At present, this area is disconnected from the Beagle Channel and is occupied by fresh water. The exposed profile of the LR site is a greyish silty massive bed 3.0 m above sea level (a.s.l.) radiocarbon dated by Gordillo *et al.* (1993) at 7518 +/- 58 BP (NZ # 7730). Shells of the RO were dated by Rabassa *et al.* (1986) at 4425 +/- 55 BP (SI # 6735). The ER and the LV sites can be correlated, according to their elevation (near 2.5 - 3.0 m a.s.l.), with the Río Ovando site. In the central sector the existence of a profile with molluscs in life position close to the Golondrina bay (BG; Fig. 1), 5 km east of Ushuaia, must be mentioned. Finally, in the eastern sector, molluscs without signs of transportation near 3 m above m.s.l. were also found on Gable Island (IG; Fig. 1).

MATERIAL AND METHODS

Molluscs from each assemblage mentioned in Figure 1, *i.e.* LR, RO, ER, LV, BG and IG, were identified, counted and measured in size. Shell size range (SSR) of the main taxa, relative abundance of the articulated valves (AV) and orientation of the shells (life position or horizontal position) were calculated. Biodiversity of the preservable groups was also considered. The Shannon index (H') as an estimate of species richness was coupled with the Shannon evenness (E) as a measure of evenness and with the Simpson index (D) as a measure of dominance. Diversity was calculated separately for each assemblage. High values of the Shannon index indicate a combination of many species and an even distribution of the specimens over the species. In relation to evenness, values close to the maximum of 1 show uniform abundances of the taxa. Finally, as dominance increases diversity decreases (see equations in Magurran, 1988).

Complementary observations of modern benthic communities of the Beagle Channel were made in the intertidal zone at low-water mark in the sublittoral zone by means of SCUBA diving, and under laboratory conditions at the aquarium of the CADIC. Material was collected during March and October 1988.

TABLE 1. – List of the total fauna of molluscs collected in the studied area.

Class GASTROPODA Cuvier 1797
Subclass PROSOBRANCHIA Milne Edwards 1848
Order ARCHAEOGASTROPODA Thiele 1925
Family PATELLIDAE Rafinesque 1815
<i>Nacella magellanica</i> (Gmelin 1790)
<i>Nacella deaurata</i> (Gmelin 1790)
Family TROCHIDAE Rafinesque 1815
<i>Calliostoma</i> (Swainson 1840) sp.
<i>Margarella violacea</i> (King & Broderip 1831)
Order MESOGASTROPODA Thiele 1925
Family LITTORINIDAE J.E. Gray 1840
<i>Eatoniella kerguelensis</i> (Smith 1875)
Family CERITHIDAE Fleming 1822
<i>Ataxocerithium pullum</i> (Philippi 1845)
<i>Eumetula michaelsoni</i> (Strebel 1906)
Family CALYPTRAEIDAE Blainville 1824
<i>Calyptraea pileolus</i> d'Orbigny 1841
<i>Crepidatella dilatata</i> (Lamarck 1822)
Family NATICIDAE Forbes 1828
<i>Falsilunatia limbata</i> (d'Orbigny 1840)
Order NEOGASTROPODA Thiele 1929
Family MURICIDAE Rafinesque 1815
<i>Trophon geversianus</i> (Pallas 1774)
<i>Xymenopsis muriciformis</i> (King 1831)
Family BUCCINIDAE Rafinesque 1815
<i>Met euthria martensi</i> (Strebel 1905)
<i>Pareuthria plumbea</i> (Philippi 1845)
Subclass PULMONATA Cuvier 1797
Order BASOMMATOPHORA Schmidt 1855
Family SIPHONARIIDAE Gray 1840
<i>Siphonaria lessoni</i> (Blainville 1824)
Class BIVALVIA Linné 1758
Subclass PALAETAXODONTA Korobkov 1954
Order NUCULOIDA Dall 1889
Family MALLETIIDAE H. & A. Adams 1858
<i>Malletia cumingi</i> (Hanley 1860)
Family Nuculanidae H. & A. Adams 1858
<i>Nuculana striata</i> (King 1831)
Subclass PTERIOMORPHA Beurlen 1944
Order PTERIOIDA Newell 1965
Family PECTINIDAE Rafinesque 1815
<i>Chlamys patagonica</i> (King & Broderip 1831)
Family LIMIDAE Rafinesque 1815
<i>Limatula pygmaea</i> (Philippi 1845)
Order MYTILOIDA Férussac 1822
Family MYTILIDAE Rafinesque 1815
<i>Mytilus edulis chilensis</i> Hupé 1854
<i>Perumytilus purpuratus</i> (Lamarck 1797)
<i>Aulacomya atra</i> (Molina 1782)
Subclass HETERODONTA Neumayr 1884
Order VENEROIDA H. & A. Adams 1856
Family LEPTONIDAE J.E. Gray 1847
<i>Neolepton cobbi</i> (Cooper & Preston 1910)
Family MONTACUTIDAE Clark 1855
<i>Mysella cf. arturi</i> (Cooper & Preston 1910)
Family CONDYLOCARDIIDAE Bernard 1896
<i>Carditella naviformis</i> (Reeve 1843)
<i>Carditopsis flabellum</i> (Reeve 1843)
Family MACTRIDAE Lamarck 1809
<i>Mulinia edulis</i> (King 1831)
Family SOLENIDAE Lamarck 1809
<i>Ensis macha</i> (Molina 1782)
Family VENERIDAE Rafinesque 1815
<i>Tawera gayi</i> (Hupé 1854)
<i>Eurhomalea exalbida</i> (Chemnitz 1795)
<i>Ameghinomya antiqua</i> (King 1831)
Order MYOIDA Stoliczka 1870
Family HIATELLIDAE Gray 1824
<i>Hiatella solida</i> (Sowerby 1834)

TABLE 2. — Characteristics of the six palaeocommunities identified here with regard to shell size range (SSR), relative abundance of articulated valves (AV), and orientation/ preburial transport .

LOCALITIES and DOMINANT SPECIES	SSR (mm)	AV (%)	ORIENTATION/ PREBURIAL TRANSPORT
1. Lago Roca (LR) <i>Chlamys patagonica</i>	07 - 80	100	horizontal position / low transport
2. Río Ovando (RO) <i>Tawera gayi</i> <i>Hiatella solida</i>	12 - 38 31 - 51	100 100	life position / in situ life position / in situ
3. Entre Ríos (ER) <i>Tawera gayi</i> <i>Hiatella solida</i>	04 - 31 32 - 46	0* 0*	horizontal position / low transport horizontal position / low transport
4. Laguna Verde (LV) <i>Ameghinomya antiqua</i> <i>Hiatella solida</i>	59 - 71 35 - 44	100 100	life position / in situ life position / in situ
5. Ba. Golondrina (BG) <i>Ameghinomya antiqua</i> <i>Ensis macha</i>	n/c 95 - 135	100 100	life position / in situ life position / in situ
6. Isla Gable (GA) <i>Tawera gayi</i>	12 - 31	0*	horizontal position / in situ

* ratio of opposite valves is near 1:1.

RESULTS

All of the gastropods and bivalves sampled as subfossils are listed in Table 1. Table 2 shows characteristics of the palaeocommunities identified here with regard to shell size range (SSR), relative abundance of articulated valves (AV), and orientation/ preburial transport. In addition, Table 3 shows the living and non-preserved organisms associated with shallow molluscs in the Beagle Channel. For the trophic analysis, the life habit and feeding type are also considered in the table.

Based on previous information in the literature (Castilla, 1985; Comoglio, pers. comm.; Gordillo, 1994, 1995; Gordillo and Isla, 1991; Humphrey *et al.*, 1970; Ojeda and Santelices, 1984) and new observations, Figure 2 summarizes the probable trophic relationships of the subfossil molluscs from the Beagle Channel. Taking into account all the information, the following reconstruction of the Holocene palaeocommunities is proposed.

The *Chlamys patagonica* palaeocommunity (Fig. 3A)

This is the most diverse assemblage recognized in the data set and is characterized by the dominance of *Chlamys patagonica*. This disturbed-neighborhood (parautochthonous) assemblage consists of shell deposits with evidence of minimal shell transport. Shell material comprises whole specimens that are well preserved and non-abraded. The long, fragile *Chlamys* shells suggest a quiet-water environ-

TABLE 3. — Living and non-preserved organisms associated with shallow-water molluscs in the Beagle Channel. EP: epifaunal; IN: infaunal; VAG: vagrant; PR: producer; SF: suspension feeder; CAR: carnivorous; DF: deposit feeder.

Taxa	Life habit	Trophic group
<i>Macrocytis pyrifera</i>	EP	PR
<i>Lessonia</i> sp.	EP	PR
<i>Ulva</i> sp.	EP	PR
<i>Cladophora</i> sp.	EP	PR
<i>Iridaea</i> sp.	EP	PR
<i>Nothogenia</i> sp.	EP	PR
unidentified sponges	EP	SF
unidentified anemones	EP	CAR
spirobid annelids	EP	SF
serpulid annelids	IN	SF
<i>Lithodes santolla</i>	VAG	CAR
<i>Paralomis granulosa</i>	VAG	CAR
<i>Halicarcinus planatus</i>	VAG	CAR
unidentified spp.	EP	SF
<i>Cosmasterias lurida</i>	VAG	CAR
<i>Patiria</i> sp.	VAG	CAR
<i>Pseudechinus magellanicus</i>	VAG	DF
<i>Austrolycus depressiceps</i>	VAG	CAR
<i>Patagonotothen tessellata</i>	VAG	CAR

ment. Articulated valves indicate minimal current transport.

Besides the main taxa considered in Figure 3A, other molluscs such as *Ameghinomya antiqua*, *Tawera gayi* and *Nuculana striata* appeared as single valves and were interpreted as part of the shelly covered substratum. No attempt was made to count specimens less than 5 mm -such as micro-molluscs, juvenile molluscs, foraminifers and ostracods- because they are considered part of the sediment fraction. Barnacles and young specimens of the brachiopod *Magellania venosa* were not

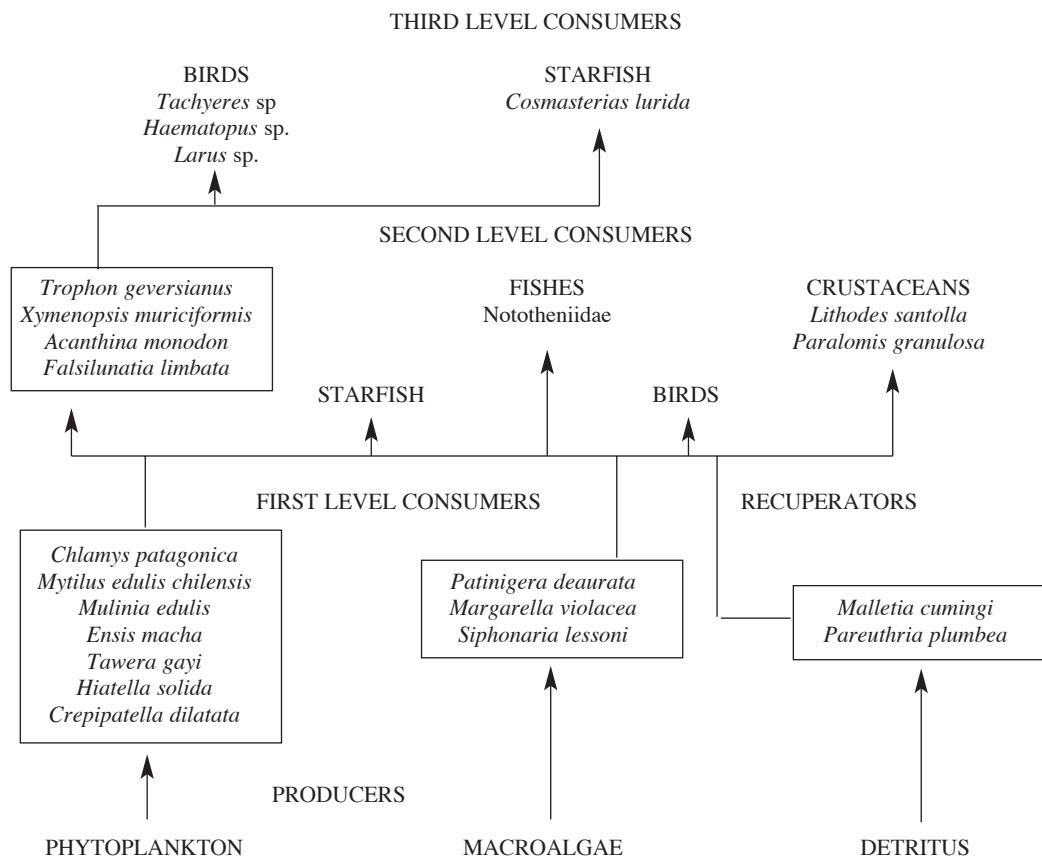


FIG. 2. – Probable trophic relationships of the subfossil molluscs from the Beagle Channel. Molluscs are listed within rectangles.

counted because they are considered as forming part of the epibiontic community of bivalves. Living specimens of *Chlamys patagonica* from Bahía Ushuaia have valves covered by epibionts, which mainly consist of non-preserved organisms. These include limpets, barnacles, bryozoans, encrusting sponges and the agglutinated tubes of spirorbid annelids. Only limpets and barnacles are preserved as subfossils. These groups form dense clusters on the *Chlamys* left valve (upper surface). The dominant species *Chlamys patagonica*, barnacles and other bivalves are epifaunal suspension feeders. Other trophic types less represented include grazers, predators and detritus feeders. The highest biodiversity value (2.12) corresponds to this epifaunal palaeocommunity. The lower dominance of this palaeocommunity is indicated by the lowest value of 0.24. A great similarity between this palaeocommunity and modern ones described by other authors (McCammon and Buchsbaum, 1968; Valladares and Andrade, 1990; Privitera, 1992) for the Magellan Straits (Tierra del Fuego) is apparent.

The *Tawera gayi* palaeocommunity (Fig. 3B)

This association is composed of several species of semi-infaunal and infaunal bivalves and gastropods. Other common groups are epifaunal brachiopods and barnacles. The *Tawera gayi* association was described from the Río Ovando (RO; $n=98$), Isla Entre Ríos (ER; $n=99$) and Isla Gable (GA; $n=42$) sites. Figure 3 B shows a reconstruction of the *Tawera gayi* palaeocommunity at the Río Ovando site. Other groups are micromolluscs (*Limatula pygmaea*; *Carditella naviformis*; *Carditopsis flabellum*), foraminifers and ostracods, but they were not counted (for the same reasons as described above). Ophiuroids and echinoids are represented commonly as isolated ossicles and spicules. Finally, barnacles -as epibionts of bivalves- are also a main component of the mollusc assemblages. *Tawera gayi* and *Hiatella solida* are the dominant species at the different localities considered, although there are some differences in the subdominant species. The small clam *Tawera gayi* is a semi-

infaunal suspension feeder, which lives partially buried within the sandy subtidal in depths of 2-10 m. In contrast, *Hiatella solida* is known to have great variability in its life habits and habitats (it also lives in the epifaunal palaeocommunity). In the Beagle Channel, it lives attached to pebbles, shells and kelp, or partially buried - as a free form - on sandy and finer sediments (Gordillo, 1995). The presence of *Tawera gayi* at the Cormoranes Archipelago suggests shallow subtidal conditions and depths of 1-10 m for the assemblages. Due to the presence of *Siphonaria lessoni*, the GA locality may be regarded as a very shallow water environment. The presence of fragments of mytilids at the ER site suggests some physical mixing of faunas from rocky envi-

ronments. From a trophic viewpoint, suspension feeders, grazers and carnivores make up 80-90%, 5-10% and 1-5% of the individuals in the *Tawera gayi* associations respectively. Near-normal marine salinity is indicated by the presence of venerid bivalves. At present times, the *Tawera gayi* association is a typical shallow-water community of sandy sediments in the Beagle Channel.

The *Ameghinomya antiqua*-*Hiatella solida* palaeocommunity (Fig. 3C)

This association is described for the Laguna Verde (LV; n=32) site. Similar to other venerids, *Ameghinomya antiqua* cannot tolerate brackish and estuar-

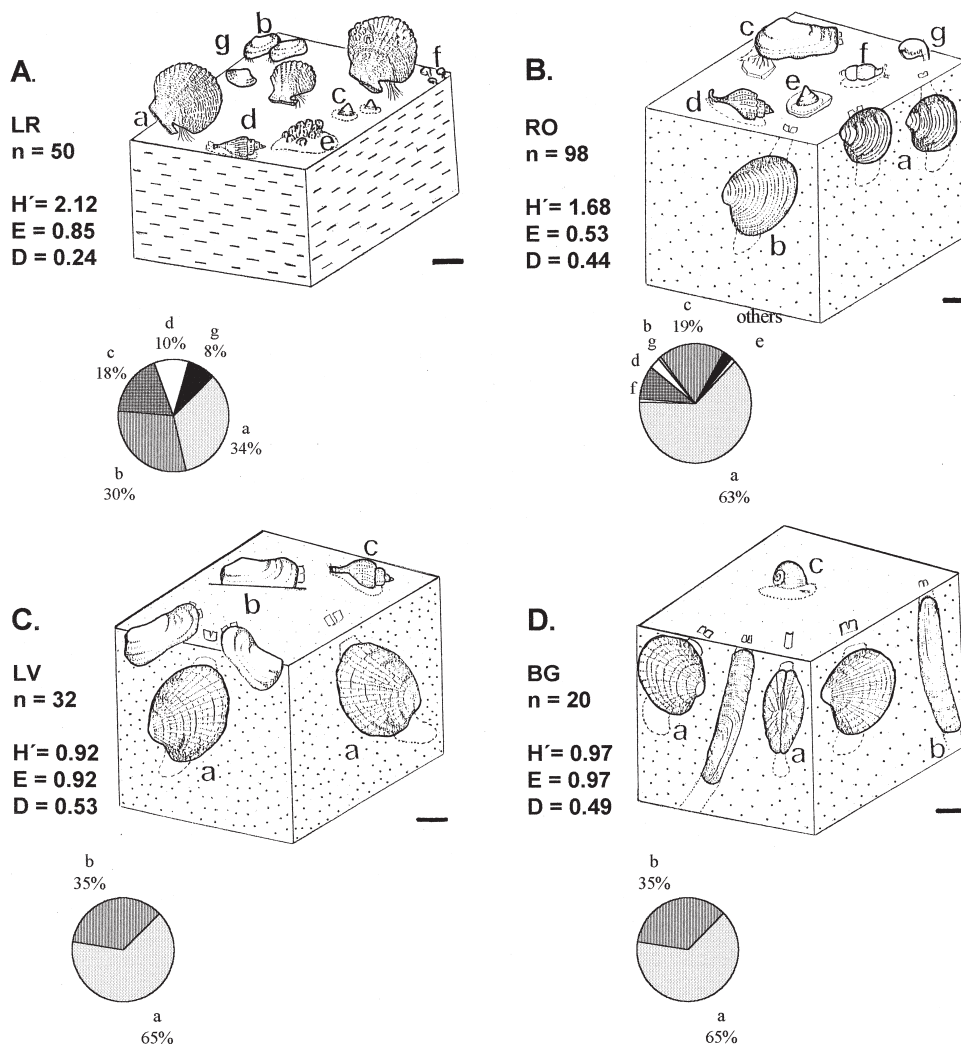


FIG. 3. – Frequency of occurrence of the main taxa; biodiversity indices and reconstruction of the Holocene molluscan palaeocommunities in the studied area. (A). *Chlamys patagonica* palaeocommunity. a: *C. patagonica*; b: *Hiatella solida*; c: *Calyptrea pileolus*; d: *Trochon geversianus*; e: barnacles and f: *Magellania venosa* (brachiopod). (B). *Tawera gayi* palaeocommunity. a: *T. gayi*; b: *Eurhomalea exalbida*; c: *Hiatella solida*; d: *Trochon geversianus*; e: *Calyptrea pileolus*; f: *Pareuthria plumbea* and g: *Magellania venosa*. (C). *Ameghinomya antiqua*-*Hiatella solida* palaeocommunity. a: *A. antiqua*; b: *H. solida*; c: *Trochon geversianus*. (D). *Ameghinomya antiqua*-*Ensis macha* palaeocommunity. a: *A. antiqua*; b: *E. macha* and c: *F. limbata*. See explanations of the diversity indices in the text. Scale 20 mm.

ine environments, so this palaeocommunity also falls within the normal water salinity mentioned for this geographic area. It inhabits coarse sandy waters at depths between 2 m and 10 m. The trophic structure of this community is marked by an abundance of infaunal suspension feeders. The existence of drilled shells in the sediment fraction and the presence of drilling gastropods (muricids and naticids) in benthic modern communities of the region suggests that drilling gastropods are also part of this palaeocommunity.

The *Ameghinomya antiqua-Ensis macha* palaeocommunity (Fig. 3D)

The *Ameghinomya antiqua-Ensis macha* association is described for the Bahía Golondrina (BG; $n=20$) site. Differences in composition from the *Ameghinomya antiqua-Hiatella solida* association of the LV site may be due to a slightly deeper environment in this case, because *E. macha* lives in deeper subtidal water (10 m) within sandy substrata. Infaunal living communities that include *Ameghinomya antiqua* and *Ensis macha* were described by Urban (1994) from the Bay of Dichato at the Pacific ($36^{\circ} 32' S$, $73^{\circ} 57' W$). This author correlates the distribution pattern of six infaunal bivalves with that of the sediment grain sizes: *i.e.* at one station (CM) with coarse sand as well as very fine sediments only *Ameghinomya antiqua* was present, whereas at another station (PH) the sediments were finer and only *Ensis macha* and the bivalve *Tagelus dombeii* were found. Thus, in life, the two species inhabit different patches within the same environment, but as fossil (our data) the species coexist within the same substrata, showing that coexistence is partly related to their different adaptations to the grain size (horizontal zonation). Another element that controls the coexistence of these filter feeding species, which compete for space and food, is also considered by Urban (1994). This author concludes that different burrowing depths in the substratum (vertical zonation) reduce competition between the two species and permit coexistence in the same environment. Thus, this observation would be applicable to the association described here, since *Ameghinomya antiqua* is a shallow burrowing and *Ensis macha* a deep burrowing species. As seen above, the trophic structure of this community is also marked by an abundance of infaunal suspension feeders. No other trophic groups were found, but *Ensis macha* can be consid-

ered ecologically equivalent to *Ensis directus* from the Northern Hemisphere, described by Frey *et al.* (1986). These authors mentioned that *E. directus* is a prey of the naticid *Polinices duplicatus*, which captures its prey by attacking its foot rather than by drilling through the shell. The gastropod *P. duplicatus* would be ecologically equivalent to *Falsilunatia limbata* from the Beagle Channel. Consequently, it is possible that the naticids prey on *E. macha* without evidence of drilling. Evenness in these *Ameghinomya antiqua* palaeocommunities reaches the highest values and hence the diversity is less than that of the other palaeocommunities.

CONCLUSIONS

The molluscan assemblages indicate that little or no *postmortem* transportation has taken place, so they represent accurately the distribution of living populations from which they were derived. All these associations suggest shallow, subtidal, cold-temperate environments. An epifaunal *Chlamys patagonica* palaeocommunity (ca. 8,000-7,000 BP) and three infaunal (*Tawera gayi*; *Ameghinomya antiqua-Hiatella solida*; and *Ameghinomya antiqua-Ensis macha*) palaeocommunities (ca. 4,400-4,000 BP) are recognized. In spite of the different relative ages of these palaeocommunities, and based on the knowledge that a warmer intermediate period took place ca. 6,000-4,500 BP, coinciding with the highest sea level, they must have developed in two similar relatively cool periods (*i.e.* before and after the Hypsithermal).

The *Chlamys patagonica* palaeocommunity is the most diverse assemblage recognized, and is also characterized by the presence of preservable and non-preserved epibionts including limpets, barnacles, bryozoans, encrusting sponges and spirorbid annelids. On the other hand, infaunal palaeocommunities exhibited less diverse values, with the minimum diversity corresponding to the *Ameghinomya antiqua-Ensis macha* palaeocommunity.

Reconstruction of trophic structure based primarily on characteristics of living taxa shows that the Holocene benthic palaeocommunities were composed of infaunal and epifaunal-suspension feeding bivalves, and a minor component of deposit feeders. Among gastropods there were detritus collectors, swallowers and carnivores. Predators of molluscs probably include starfish, crabs, drilling gastropods, nototheniid fish and birds.

Finally, based on comparisons with modern benthic communities in this region, these associations show no evidence of dramatic ecologic and climatic changes during the period considered (ca. 8,000 - 4,000 BP). After deglaciation, these faunas apparently occupied the new vacant niches, and minor climatic changes during this very brief period could not be enough to produce significant changes in the faunal composition of these wide temperate-cold distributed species. Thus, a postglacial succession of faunas is not evidenced from these data, suggesting an apparent stability of modern marine communities over a period of several thousand years.

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