A Late Pleistocene macrobenthic assemblage in Caleta Patillos, northern Chile: paleoecological and paleobiogeographical interpretations

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ABSTRACT. In the present study, we describe and analyze the structure of a Late Pleistocene (likely last interglacial) marine macrobenthic assemblage in Caleta Patillos (20°45'S, 70°12'W), northern Chile. A taphonomic analysis suggests the existence of a shallow subtidal paleoenvironment, mainly soft-bottom, of high energy and intense mixing from several benthic habitats. The total number of 38 taxa recorded, mainly gastropods and bivalves, was not different than the ones reported in other late Pleistocene assemblages in northern Chile. At a biogeographic scale, the composition of mollusk species showed remarkable similarities with present-day fauna, and no extralimital species were recorded. At local scale, however, a comparison with the living assemblage in the same area of study showed a dramatic shift in the species' composition, a result that cannot be explained by sampling bias. A deep and perhaps very recent (*i.e.,* at historical times) alteration of the structure of local macrobenthic assemblages is hypothesized.

Key words: Late Pleistocene, Fossil Assemblage, Caleta Patillos, Mollusks, Northern Chile.

RESUMEN. **Un ensamble macrobéntico del Pleistoceno tardío en Caleta Patillos, norte de Chile: interpretaciones paleoecológicas y paleobiogeográficas.** En este trabajo se describe y analiza la estructura de un ensamble fósil marino macrobentónico del Pleistoceno Tardío (posiblemente último interglacial) en Caleta Patillos, norte de Chile (20°45'S, 70°12'O). Un análisis tafonómico sugiere la existencia de un ambiente de depositación submareal somero, primariamente de fondo blando, de alta energía, e intensa mezcla de especies desde varios tipos de hábitats bentónicos. El total de 38 taxa identificados, correspondientes en su mayoría a especies de moluscos, gastrópodos y bivalvos, no fue distinto de lo registrado en otros ensambles pleistocénicos tardíos en el norte de Chile. A una escala biogeográfica, la composición del ensamble de moluscos mostró notables similitudes con la fauna actual, y no se registraron especies extralimitales. A una escala local, sin embargo, una comparación con el ensamble viviente en el mismo sitio de estudio mostró una dramática alteración en la composición de especies, un resultado que no puede ser explicado por sesgos de muestreo. Se plantea una profunda y quizás muy reciente (*i.e.,* en tiempos históricos) alteración en la estructura de los ensambles macrobentónicos locales.

Palabras claves: Pleistoceno tardío, Ensamble fósil, Caleta Patillos, Moluscos, Norte de Chile.

1. Introduction

Although the first studies of macrofossil assemblages in northern Chile can be dated to Charles Darwin (1846) and Rodulfo Philippi (1887), the bases of the modern knowledge of marine Quaternary fauna in the region can be attributed to Dietrich Herm and his seminal monograph (Herm, 1969). A plethora of studies done by Luc Ortlieb and colleagues (Ortlieb *et al.*, 1990, 1994, 1995, 1997a, 1997b; Paskoff *et al.*, 1995; Guzmán *et al.*, 2000) in the last decade have provided a much more complete picture of the structure of Quaternary mollusk faunas represented in the last four interglacial periods.

The mollusk assemblages described for the last interglacial period, ~85-125 Kyr BP, reveal large similarities in the species' composition with the modern counterparts in the region (Ortlieb *et al.*, 1994, 1995; Guzmán *et al.*, 2000). However, those studies have been geographically concentrated between 22° and 30°S in Chile, and *ca.* ~17°S in Perú (Ortlieb *et al.*, 1990, 1994, 1995; Guzmán *et al.*, 2000), leaving a large gap of ~500 km between Ilo, Perú and Mejillones, in northern Chile, completely unstudied. The structure of the local assemblages in the gap region might not be the same that the one found in known sites, due to the relatively uniform topography of the coast, with very few and only small embayments, and a predominance of wave-exposed environments (Brattström and Johanssen, 1983; Camus, 2001). Therefore, filling this gap might be crucial to fully understand the spatial-temporal patterns exhibited by past benthic assemblages. Indeed, it has been hypothesized, but not yet tested, that there was a past biogeographic break ~18°S (Ortlieb *et al.*, 1994) within the gap area. Radtke (1989) and Rivadeneira (2005) confirmed the presence of late Pleistocene and Holocene marine terraces in the region of Iquique, but to date no single study has described the existing macrofaunal assemblages.

The studies of the Quaternary mollusk assemblages in the region have used species inventories to infer paleoceanographic conditions (Ortlieb *et al.*, 1994, 1995, 1996). However, the description of other key attributes of the local assemblage, as species relative abundances, and detailed accounts of paleoenvironmental conditions, have been less explored (*e.g.,* Herm, 1969). Indeed, taphonomic

studies offer a great potential to reconstruct past environments (Kidwell and Bosence, 1991) and to analyze patterns of species relative abundances in the fossil record (Kidwell, 1998, 2001). The great preservation potential of the Quaternary fossil assemblages of northern Chile represents an excellent opportunity to apply these ideas and increase our understanding of the structure and dynamics of local assemblages through evolutionary timescales.

In the present study we describe a Late Pleistocene marine macrobenthic assemblage in Caleta Patillos, in the previously unstudied region of Iquique. Our goals are: **a.** to describe the composition of the macrobenthic assemblage, **b.** to characterize the main taphonomic features of the assemblage and **c.** to evaluate the paleoecological and paleobiogeographic implications of our findings. We show that the combination of the traditional generation of species inventories combined with estimations of species relative abundances lead to more robust interpretations about the structure and dynamics of the past assemblages.

1.1. Methods

1.1.1. Data collection

The sampling was carried out in July 2004 in a marine terrace located at Caleta Patillos (20°45'S, 70°12'W, 12 m a.s.l., Fig. 1). A total of 20 samples of *ca*. 1 l were taken. Bulk samples were obtained from the upper 25 cm of the sediment, and sieved *in situ* using a 2 mm standard sieve. Each sample was individually analyzed in laboratory. Fossil individuals were identified to the lowest taxonomic level possible, based on authorities: Ramorino (1968), Herm (1969), Keen (1971), Marincovich (1973), Larraín (1975), Ramírez (1993), Guzmán *et al.* (1998), Reid and Osorio (2000), Espoz *et al.* (2004), and all individuals present in the sample were counted. In the case of bivalves, we assumed that individual valves corresponded to different individuals (*e.g.,* Todd *et al.*, 2001). In the case of highly fragmented remains, when it was not possible to count individuals, we recorded the presence of species/taxa in the sample.

Since the quality of preservation of some taxa was low, and only fragments were recovered, their individual abundance could not be estimated directly. In order to circumvent this problem, we used their relative occurrence as a proxy of the total
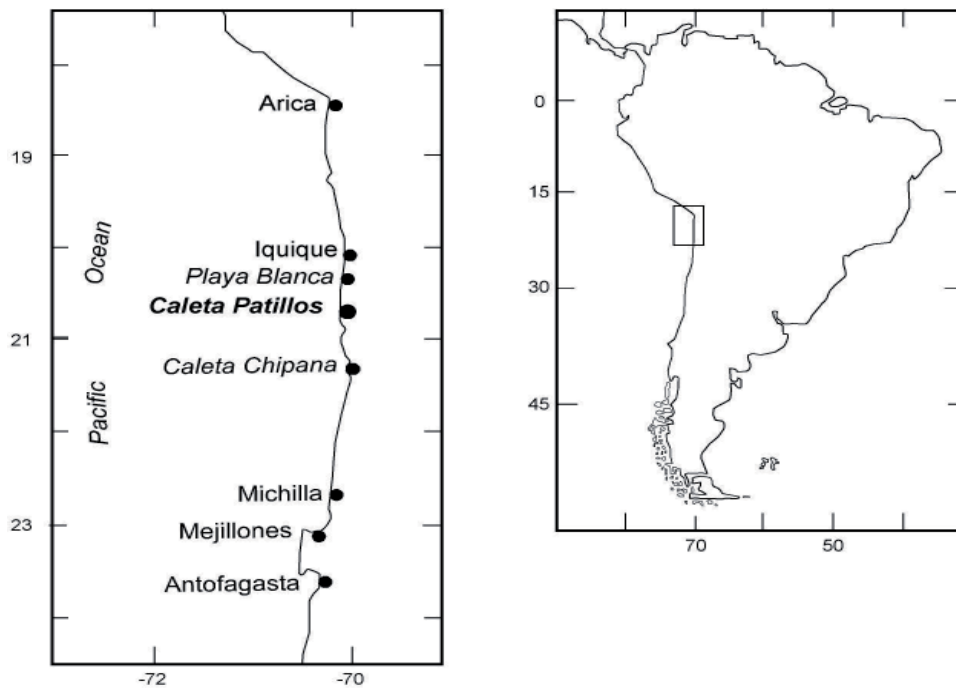
FIG 1. Map showing the study site, Caleta Patillos, and other sites located in northern Chile mentioned in the text.

number of individuals. Considering that the relationship between species abundance and occupancy is a very widespread phenomena in both ecological and fossil assemblages (Gaston and Blackburn, 2000; Buzas and Culver, 2001), the use of sampling occurrence data as a proxy of total species abundance is very advisable. In fact, for a subset of 31 species, the occurrence across samples is a very good predictor of the total number of individuals recorded (number of individuals=0.9173*number of samples $^{1.4118}$, r²=0.93, p<0.001, n=31). Therefore, the occurrence of species across samples can be considered as a reliable estimator of their abundance. Since recent advances in the study of taphonomic processes indicate that relative abundance of fossil remains might be a true reflection of the original living assemblage (Kidwell, 2001), the observed patterns of dominance are likely to be true.

1.1.2. Age of the assemblage

Although we do not have a direct age estimation of the site, several lines of evidence suggest a Late Pleistocene, probably last interglacial age. For instance, Th/U and ESR radiometric dating done by Radtke (1989) in a marine terrace at Playa Blanca, located only ~45 km north of the study site, revealed ages of 96.400-118.000 BP for a same height (12 m a.s.l.). Local tectonic events were not evident. Similarly, several terraces in the zones of Antofagasta and Mejillones have yielded last interglacial ages for similar heights (Radtke, 1987, 1989; Ortlieb *et al.*, 1995). Thus, a preliminary last interglacial assignation for the site seems well supported.

1.1.3. Taphonomic analysis

We analyzed the main taphonomic features of the fossil assemblage in order to reconstruct paleoenvironment conditions, and the *post-mortem* processes affecting macrofossils. On the one hand, species were classified according to their known modern bathymetric distribution (intertidal, subtidal, both) and type of substrate (hard, soft bottom, both), based on literature information (Ramorino, 1968; Marincovich, 1973; Keen, 1971; Ramírez, 1993; Guzmán *et al.*, 1998; Reid and Osorio, 2000). On the other hand, we estimated the proportion of left/right valves of *Mulinia edulis* (King and Broderip), the dominant species in the assemblage (see Table 1) as an indicator of the energy or transport in the *post-mortem* paleoenvironment (Feige and Fürsich, 1991). Departures from a null expectation (using a Chi-square

TABLE 1. LIST OF TAXA RECORDED IN THE STUDY AREA AND MAIN PALEOECOLOGICAL FEATURES.

Species/taxa	Abundance		Habitat [1]		Substrate [1]		Modern Geographic Distribution [1]		Quat. Fossil Record [2]
	N	%	I	S	H	S	R	E	
Polyplacophora									
Enoplochiton niger (Barnes)	f	10	o		o		o		Nd
Chiton sp.	f	5	Na	Na	o		Na	Na	Na
Bivalvia									
Aulacomya ater (Molina)	3	15	o	o	o		o		o
Choromytilus chorus (Molina)	f	85		o	o		o		o
Glycymeris ovatus (Broderip)	3	15		o		o	o		o
Mesodesma donacium (Reeve)	5	15	o	o		o	o		o
Mulinia edulis (King and Broderip)	204	100	o	o		o	o		o
Protothaca thaca (Molina)	25	40	o	o		o	o		o
Nuculana cuneata (Sowerby)	2	10		o		o	o		
Semele solida (Gray)	1	5	o	o		o	o		o
Tagelus dombeii (Lamarck)	1	5	o	o		o	o		o
Venus antiqua (King and Broderip)	1	5	o	o		o	o		o
Veneridae indet (juvenile)	1	5	Na	Na	Na	Na	Na	Na	Na
Gastropoda									
Calyptraea trochiformis (Born)	18	60	o	o	o		o		o
Concholepas concholepas (Bruguière)	2	10	o	o	o		o		o
Crassilabrum crassilabrum (Sowerby)	9	30	o	o	o		o		o
Crepidula dilatata (Lamarck)	124	95	o	o	o		o		o
Echinolittorina peruviana (Lamarck)	1	5	o	o	o		o		o
Fissurella pulchra (Sowerby)	1	5	o	o	o		o		
Fissurella sp. (juvenile)	4	15	Na	Na	o		Na	Na	Na
Mitrella unifasciata (Sowerby)	30	85	o	o	o		o		o
Nassarius gayi (Kiener)	49	85		o		o	o		o
Oliva peruviana (Lamarck)	22	60		o		o	o		o
Polinices uber (Valenciennes)	9	45	o	o		o	o		o
Priene scabrum (King)	1	5		o		o	o		o
Prisogaster niger (Wood)	5	10	o	o	o		o		o
Scurria ceciliana (d'Orbigny)	1	5	o		o		o		o
Scurria orbignyi (Dall)	1	5	o		o		o		o
Scurria scurra (Lesson)	16	30	o		o		o		o
Scurria sp. (juvenile)	3	15	o		o		Na	Na	
Tegula luctuosa (d'Orbigny)	2	10	o	o	o		o		o
Tegula quadricostata (Gray)	1	5		o	o		o		o
Tegula tridentata (Potiez and Michaud)	1	5	o	o	o		o		o
Turritella cingulata (Sowerby)	2	10		o	o		o		o
Cirripedia									
Austromegabalanus psittacus (Molina)	f	80	o	o	o		o		o
Balanus cf. flosculus Darwin	f	15	o	o	o		Na	Na	o
Decapoda									
Indeterminatae	f	5	Na	Na	Na	Na	Na	Na	Na
Echinoidea									
Cf. Tetrapygus niger (Molina)	f	80	o	o	o		o		o

Abundance (**N**: number of individuals; **%**: percentage of individuals, **f**: abundance estimated from occurrence data (see methods). Habitat (**I**: intertidal, **S**: subtidal). Substrate (**H**: hard bottom, **S**: soft bottom). Modern geographic distribution (**R**: resident in the area; **E**: extralimital, not recorded in the area). Occurrence in the Pleistocene and Holocene fossil record of northern Chile and southern Perú (Quaternary fossil record). **o**: present. **Nd**: no data. **Na**: not applicable.

[1] Ramorino (1968), Marincovich (1973), Keen (1971), Larraín (1975), Ramírez (1993), Guzmán *et al.* (1998), Reid and Osorio (2000), Espoz *et al.* (2004);

[2] Herm (1969), DeVries and Wells (1990), Ortlieb *et al.* (1990, 1994, 1995, 1997a, 1997b), Paskoff *et al.* (1995), Guzmán *et al.* (2000).

test) can be used to infer high energy *post-mortem* environments (Feige and Fürsich, 1991).

1.1.4. Diversity of the assemblage

The quality of species inventory was assessed using a rarefaction analysis (Estimates, Colwell, 2005), based on occurrence data. The same data was used to estimate the 'true' richness, using the Chao 2 extrapolation index (Colwell, 2005). The richness and composition of gastropod and bivalve species were compared with other Late Pleistocene assemblages of southern Perú and northern Chile using previously reported studies (Ortlieb *et al.*, 1990, 1994, 1995). This restriction was made since these two taxa are the best studied, and hence, the most comparable.

The mollusk species composition was also compared with present-day assemblages, at two different spatial scales: **i)** regional and **ii)** local. First, to evaluate regional-scale (biogeographic) changes in the composition we used the modern latitudinal distribution reported for each species in the literature (see references in *Data collection*). In particular we evaluated the presence of species with present-day latitudinal ranges not overlying the study area, the so-called 'extralimitals' (*sensu* Roy *et al.*, 1995). A large presence of extralimitals in the fossil assemblage could be used as an indication of biogeographic, large-scale changes in the composition of assemblages. Second, we compared the species composition of the fossil mollusk assemblage with the mollusk species recorded presently in the same study area. The species list was obtained by a recent monitoring (Universidad Arturo Prat[1]) that covered different shallow benthic habitats (rocky intertidal, rocky subtidal, soft subtidal), so the inventory can be considered as an exhaustive account of the present-day mollusk diversity in the study site. The similarity in species composition was assessed with the widely used Jaccard index. In order to control for possible preservation bias, we performed the analysis only with those present-day species that have been recorded in the Quaternary fossil record of the Southeastern Pacific (obtained from an exhaustive literature review). Since differences in the total number of species recorded in both assemblages (derived by an incomplete sampling) may also bias the analysis, we performed a simply numerical experiment in order to get a species number-corrected Jaccard estimation. This was done by randomly taking 29

species (the number of mollusk species in the fossil assemblage) from the present-day inventory which was compared with the fossil assemblage, obtaining a new estimation of the Jaccard index. The procedure was repeated 1,000 times. The resulting distribution of simulated values was used to construct a 95% confidence interval of Jaccard values.

2. Results and Discussion

The assemblage corresponds to a mixture of species inhabiting several bathymetric levels (inter and subtidal) and substrates (hard and soft-bottoms) (Table 1). The *in situ* observations showed that individuals were not in living position. Furthermore, no single articulated bivalve individual was found. Most of species (62%) correspond to species inhabiting both inter and subtidal stands, representing a mixture of soft and hard-bottom environments. The proportion of left/right valves biased, with a predominance of right valves (ratio L/R=0.67), which is marginally different from the random expectation (χ^2=3.74, g.l=1, p=0.053).

The ecological features of the described macrofauna suggest the existence of a shallow subtidal paleonvironment. However, the presence of several taxa inhabiting hard-bottom intertidal and subtidal stands indicates an important degree of horizontal and vertical transportation of shells, suggesting a 'mixed assemblage' (auto/allochthonous) (Kidwell and Bosence, 1991; Kidwell, 1998). In addition, the absence of articulated bivalves, and the lack of individuals in living position indicate a time-averaged assemblage (Kidwell and Bosence, 1991; Kidwell, 1998). This has important implications for both paleoecological and paleobiogeographical interpretations. First, this implies that comparison with present-day assemblages should be done with caution, since species from several habitats (and therefore, several assemblages) are being pooled in a single assemblage. Second, although some habitat-specific signatures might be lost in these mixed assemblages, the among-habitat pooling provides a very good picture of the overall coastal benthic biodiversity patterns, encompassing temporal scales of 100's or 1,000's of years (as suggested by the time-averaging, Kidwell, 1998), highly desirable by synoptic biogeographical and macroecological analyses.

The taphonomic analysis also indicates the existence of a high energy paleoenvironment (*i.e.,* wave

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[1] Universidad Arturo Prat, 2003. Comunidades bentónicas de Punta Patillos. *In* Evaluación de impacto ambiental Terminal 2, Puerto Patillos, I Región, Chile. Available and published at: http://www.e-seia.cl. p. 40-69.

exposed) based on: **i)** the great fragmentation of fossil material; **ii)** bias in the proportion of left/right valves of *M. edulis* (*e.g.,* Feige and Fürsich, 1991) and **iii)** the presence of several taxa inhabiting in wave exposed rocky intertidal habitats. The inner matrix is rich in cobbles and irregular stones, which also suggest paleoenvironments with a high potential of shell fragmentation. Further support to our paleonvironmental interpretation is given by the high occurrence (*i.e.,* in 80% of samples) of remains of the large barnacle *Austromegabalanus psittacus* (Molina) and of the sea urchin cf. *Tetrapygus niger* (Molina), two species typically associated to wave exposed areas in shallow hard bottom stands.

The species accumulation curve showed evidence of an incomplete saturation (Fig. 2). Thus, the total 38 taxa recorded (Table 2) should be considered as a non-exhaustive list. Indeed, a non-parametric extrapolation indicates that further sampling would increase the species inventory in *ca.* 44% (Chao 2=55 species, SD=7). Most of the recorded species belong to gastropods (55%, 21 out of 38) and bivalves (29%, 11 out of 38). Other taxa, including 2 chitons, 1 crustacean and 1 echinoid, were also recorded, but they comprised less than 13% of total richness and 15% of relative abundance. For the best represented taxa, gastropod and bivalves, the total 32 putative species recorded are not different from the mean 37 species (SD=13) recorded across 11 Late Pleistocene sites (likely of similar age to Patillos, Ortlieb *et al.*, 1994) in the area of Antofagasta (t test, t=1.366, d.f.=10, P=0.20). The richness is even higher than the reported for the site of Michilla (Ortlieb *et al.*, 1995), only *ca.* 200 km south Caleta Patillos. Furthermore, the extrapolated mollusk richness (Chao 2=44, SD=9) is quite similar to the modern richness recorded in the same site (42 species), contrary to the idea that the richness was higher during last interglacial (Ortlieb *et al.*, 1994). However, these comparisons should be interpreted with caution since differences in sampling effort are not being considered.

From a total of 29 gastropod and bivalve taxa recognized up to species level, 27 (93%) have been previously recorded in other Pleistocene terraces in northern Chile and southern Perú (Table 1). This fact is not surprising given the large amount of paleontological information collected during the last ~35 yr in northern Chile (Herm, 1969; Ortlieb *et al.*, 1994, 1995, 1996, 1997a, 1997b; Guzmán *et al.*, 2000). Although estimations of the completeness
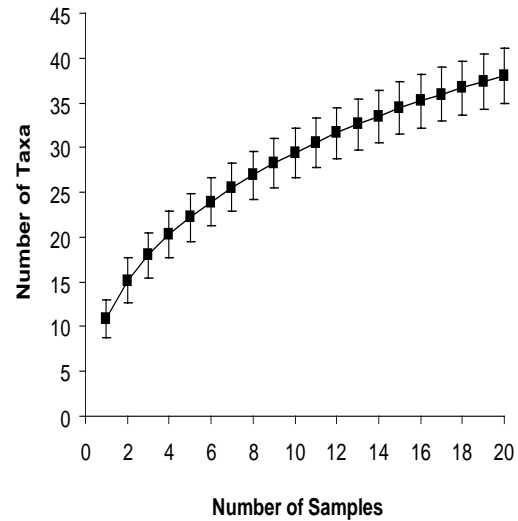

FIG. 2. Species accumulation curve for the macrobenthic assemblage of Caleta Patillos. Error bars indicate the 95% confidence intervals.

TABLE 2. MOLLUSK SPECIES (ONLY BIVALVE AND GASTROPODS CONSIDERED) RECORDED IN THE MODERN ASSEMBLAGES, BUT NOT PRESENT IN THE LATE PLEISTOCENE ASSEMBLAGE, AT CALETA PATILLOS

Taxa	Species
Bivalvia	*Argopecten purpuratus* (Lamarck)
	Brachidontes granulata (Hanley)
	Chione peruviana (Sowerby)
	Diplodonta inconspicua (Phillippi)
	Eurhomalea salinensis (Ramorino) *
	Perumytilus purpuratus (Lamarck)
	Semimytilus algosus (Gould)
Gastropoda	*Aeneator fontainei* (d'Orbigny)
	Bursa ventricosa (Broderip)
	Calliostoma fonkii (Philippi) *
	Cancellaria buccinoides (Sowerby)
	Crucibulum quiriquinae (Lesson)
	Entodesma cuneata (Gray)
	Fissurella crassa (Lamarck)
	Fissurella latimarginata (Sowerby)
	Fissurella maxima (Sowerby)
	Fissurella peruviana (Lamarck)
	Mitrella caletae (Preston) *
	Nassarius dentifer (Powys)
	Nodilittorina araucana (d'Orbigny)
	Polinices cora (d'Orbigny)
	Priene rude (Broderip)
	Scurria zebrina (Lesson)
	Tegula atra (Lesson)
	Thais chocolata (Duclos)
	Thais haemastoma (Linne)
	Trigonostoma bullatum (Sowerby) *
	Xanthochorus buxea (Broderip)

* never found in the Quaternary fossil record of the Southeastern Pacific.

of mollusk inventories are not yet available (*e.g.* Valentine, 1989; Cooper *et al*., 2006), preliminary results for bivalves in northern Chile show that ~46% of modern species described for the coastal shelf (<200 m depth) are present in the fossil record. This value is rather low compared to other well-studied regions (*e.g.,* California, ~80%, Valentine, 1989), suggesting that further paleontological surveys, particularly oriented to find small-sized forms (Valentine, 1989; Cooper *et al.*, 2006) may expand the mollusk species inventories in the region.

The composition of mollusk species in the fossil assemblage showed similarities and differences with its modern counterpart, depending on the scale of analysis. On the one hand, no major change was evident at a biogeographic scale: from the total species recorded, none can be considered as extralimital (Fig. 3). Perhaps the only species that deserve a more detailed consideration are *Scurria scurra* (Lesson), *M. edulis*, and *Choromytilus chorus* (Molina). The modern northern limit of distribution of *S. scurra* has been placed at ~24°S (Espoz *et al*., 2004), ~300 km south of the study site. However, this limit was set only recently, after the colossal ENSO 1982/83, when the populations of the brown algae *Lessonia nigrescens* Bory (the exclusive habitat of *S. scurra*) were devastated (Espoz *et al*., 2004). Previous to the ENSO 1982/83, the northern limit of the species was placed at ~10°S, in the center Peruvian coast (Espoz *et al*., 2004). The extinction of *S. scurra* seems to be part of a transient dynamic operating at an ecological timescale, and it does not likely imply a real range contraction at an evolutionary timescale. Indeed, there are indications of recovery of the northern range of distribution (M.M. Rivadeneira, personal observations). *M. edulis* and *C. chorus* have been considered as extinct in northern Chile by previous studies carried out in the last decade (Ortlieb *et al*., 1994, 1995). Indeed, neither *M. edulis* nor *C. chorus* have been recorded in benthic surveys in northern Chile (Zúñiga *et al.*, 1983; Quiroga *et al*., 1999; Palma *et al*., 2005). However, recent findings question the validity of the supposed extinction of these species at the northern region of Chile and southern Perú. *C. chorus* in currently exploited by local fishermen in Caleta Chipana, southern Iquique[2] and its identity has been confirmed by DNA analysis (Galaz, 2005). Furthermore, several persistent populations of *M. edulis* have been identified in central and southern
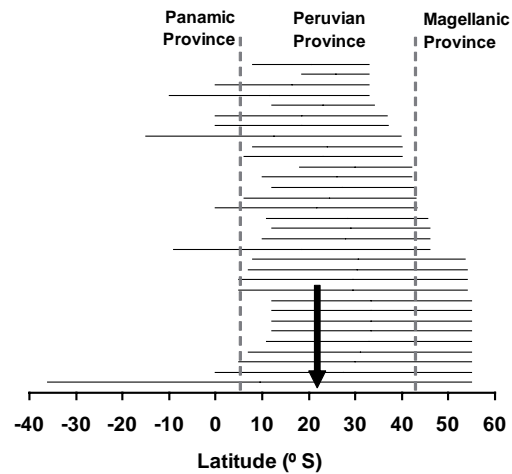

FIG. 3. Latitudinal distribution of 32 species recorded in the study. Data taken from literature (see table 1 and text). Dotted lines show the limits of the Peruvian biogeographic province, and the adjacent Panamic and Magellanic provinces. The arrow indicates the position of the study site.

Perú (Cornejo *et al*., 2005; O. Cornejo, personal communication 2007). It is uncertain whether these populations are part of a re-colonization process or if they are relicts of past populations, but again, the apparent extinction of both species may be only part of a transient dynamic. Therefore, none of these species can be considered as an extralimital form, and hence a complete similarity in species composition with present-day faunas is concluded.

Our findings are in agreement with the overall paucity of extralimital species in mollusk assemblages of northern Chile during the last interglacial (Ortlieb *et al*., 1994, 1995; Guzmán *et al*., 2000). This result is not unexpected given the fact that recent paleoceanographic reconstructions in the region suggest only slightly warmer conditions during the last interglacial (Calvo *et al.*, 2001; Molina-Cruz and Herguera, 2002; but see Teusch *et al.*, 2002). However, the absence of extralimital species in the zone is not surprising given the fact that the study area, as well as all other Pleistocene sites previously studied, are far from the known biogeographic breakpoints of the southeastern Pacific mollusk fauna (*i.e.*, ~5°S, and ~42°S, Fig. 3; Brattstrom and Johanssen, 1983; Camus, 2001). Therefore, possible migration events at scales of 100's and even 1,000's km associated to changes in paleoceanographic and/

2 Vargas, A.; Cortés, G.; Hudson, C.;Tapia, J.; Robles, R. 2004. Informe de Seguimiento 1, Área de Manejo Chipana, sector A, Iquique, Primera Región (unpublished report). SubPESCA, 20 p.+ anexos.

or paleoecological conditions simply might not have been appreciated in northern Chile (*e.g.,* Roy, 2001). The corollary is that simple regional-level species inventories can not be used to assess the stability of local assemblages during Pleistocene in the region, and moreover its use as paleoceanographic proxies should be treated with more caution.

In contrast to the biogeographic analysis, the local-scale analysis revealed a quite different picture about the stability of the mollusk assemblage (Tables 1 and 2). Only 14 species were recorded in both fossil and modern assemblages. 52% of species in the fossil assemblage (15 out of 29) were not detected in its modern counterpart. In parallel, 67% of present-day species (28 out of 42) were not detected in the fossil assemblage (Table 2), although this value may be somewhat inflated by the incompleteness of the record (see Fig. 1). Low values for the Jaccard index (J=0.25) suggest a major change in the composition of the local assemblage. Even if we remove the apparent colonizers (species present in the modern but not in the fossil assemblage) from the analysis, Jaccard values are low (J=0.48). The numerical experiment, indeed, revealed that even after corrected by differences in species richness, the estimated values of similarity remained very low (95% CI bootstrapped Jaccard values, 0.24-0.41). All these lines of evidence strongly suggest that sampling incompleteness cannot explain the large difference in species composition. This faunal change is consistent with a large change in the species relative abundance noticed in other areas of northern Chile (Ortlieb *et al.*, 1994). Therefore, even though the species composition may have remained relatively stable at a regional-scale, a much deeper variation in the structure and organization of local assemblages is hypothesized.

The lack of inertia in the species composition/species relative abundance is often reported at evolutionary timescales in different taxa and systems (see DiMichele *et al*., 2004 for a review), but the underlying processes are much less known (DiMichele *et al*., 2004; McGill *et al.*, 2005). Given the fact that we are comparing two single points in time, and we do not know the exact time when such changes occurred, a certain identification of possible causes driving the faunal turnover is quite difficult. A number of paleoceanographic conditions showed dramatic variations since the last interglacial in the region, including sea surface temperature (Calvo *et al*., 2001; Molina-Cruz and Herguera, 2002; Kim *et al*., 2002), primary productivity (Dezileau *et al*., 2004; Mohtadi and Hebbeln, 2004; Mohtadi *et al*., 2004), ENSO intensity (Sandweiss, 2003; Sandweiss *et al*., 1996, 2001; Carré *et al*., 2005), and ancient human harvesting (Llagostera, 1979; Jerardino *et al*., 1992). However, some indications suggest that the faunal turnover may have occurred, at least in part, very recently, only a few thousands or even hundreds years ago. A statistical analysis of the faunal composition of Late Pleistocene (MIS 5) and Holocene (7 ka) assemblages at the Michilla site (see table 2.2.1 in Ortlieb *et al*., 1995) revealed a remarkable similarity (J=0.88), suggesting that in spite of all environmental chances experienced during last glacial-interglacial cycle, local assemblages remained qualitatively invariant. In addition, archeological analyses show the presence of *M. edulis* and *C. chorus* in shell middens in different cultural complexes of southern Perú and northern Chile during the first centuries B.C. (Silverman, 1988; Uribe, 2006). Therefore, the loss of these 'core' species, and for extension the structure of the entire assemblage, may have occurred only in very recent times (*e.g.,* a few decades or centuries ago), perhaps similar to that observed in other marine ecosystems (Jackson, 2001; Jackson *et al*., 2001; Pandolfi *et al*., 2003; Worm *et al.,* 2006). The exact timing of these events remains, however, unsolved. Larger datasets, encompassing broader geographic and temporal scales are needed to really uncover the patterns and process regulating the structure and dynamics of Quaternary macrobenthic assemblages at the Southeastern Pacific coast.

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