

# Living (stained) calcareous benthic foraminifera from recent sediments off Concepción, central-southern Chile (~36° S)

## Foraminíferos bentónicos calcáreos vivos (teñidos) en sedimentos recientes de Concepción, Chile centro-sur (~36° S)

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### ABSTRACT

This study examines onshore-offshore and vertical distribution of living (Rose Bengal stained) benthic foraminifera (> 180 µm fraction) from three sediment stations along a bathymetric transect off Concepción, Chile (station 18 = 88 m water depth, station 26 = 120 m, station 40 = 1,030 m), within and below the oxygen minimum zone. All cores were collected in austral winter. Calcareous foraminifera dominated the three stations. The species composition, living foraminifera density, and vertical distribution patterns within the sediment changed in accordance with bottom water dissolved oxygen concentration and food availability. Onshore-offshore pattern revealed overall highest living foraminiferal densities at shelf stations 18 and 26 where bottom water dissolved oxygen was lowest (~ 0.2 mL<sup>-1</sup>) and content in labile organic matter highest. Within the sediment, maximum relative abundances (50-60 %) of living organisms were found in the 0-1 cm interval at the organic-rich and oxygen-poor shelf stations 18 and 26. In the well-oxygenated (2.7 mL<sup>-1</sup>) slope station 40, 70 % of living foraminifera were observed deeper than the first centimeter. The number of species and the contribution of the > 250 µm fraction to the total fauna larger than 180 µm increased offshore. *Nonionella auris* (d'Orbigny) dominated at stations 18 and 26 while a more diverse foraminifera fauna was found at station 40. This study provides the first quantitative data on living benthic foraminifera in the area; seasonal and interannual changes are not addressed.

**Key words:** benthic foraminifera, sediments, oxygen minimum zone, Concepción, Chile.

### RESUMEN

Este estudio examina la distribución costa-océano y vertical de los foraminíferos bentónicos calcáreos (fracción > 180 µm) vivos (teñidos) en tres estaciones a lo largo de un transecto batimétrico frente al área de Concepción, Chile (estación 18 = 88 m, estación 26 = 120 m, estación 40 = 1.030 m de profundidad), dentro y bajo la zona mínima de oxígeno. Todos los testigos de sedimento fueron recolectados durante el período de invierno. Los foraminíferos calcáreos dominaron las tres estaciones. La composición específica, distribución vertical y abundancia de foraminíferos bentónicos vivos variaron en concordancia con el contenido de oxígeno disuelto del agua de fondo y la disponibilidad de materia orgánica. El patrón batimétrico reveló una mayor densidad de foraminíferos vivos en las estaciones 18 y 26 donde el oxígeno disuelto de las aguas de fondo fue menor (~ 0,2 mL<sup>-1</sup>) y la materia orgánica lábil mayor. Dentro del sedimento, las máximas abundancias relativas (50-60 %) de foraminíferos vivos fueron encontrados en el intervalo 0-1 cm en las estaciones 18 y 26 ricas en materia orgánica y pobremente oxigenadas. En la bien oxigenada (2,7 mL<sup>-1</sup>) estación 40, el 70 % de los foraminíferos vivos se ubicaron por debajo del primer centímetro. El número de especies y la contribución de la fracción > 250 µm se incrementaron costa afuera. *Nonionella auris* (d'Orbigny) fue la especie dominante en las estaciones 18 y 26, mientras que una fauna más rica se observó en la estación 40. Este estudio proporciona los primeros datos generales acerca de la distribución de foraminíferos bentónicos vivos en el área, sin apuntar a cambios estacionales y/o interanuales.

**Palabras clave:** foraminíferos bentónicos, sedimentos, zona de mínimo oxígeno, Concepción, Chile.

## INTRODUCTION

The vertical distribution of benthic foraminifers in the sediment column seems to be determined mainly by two factors: food availability and oxygen content at the seafloor (Gooday & Rathburn 1999, Gooday 2003). This is supported by a number of field studies and experiments that demonstrate the effects of organic supply and changes in bottom water oxygen concentration on the microhabitat selection (e.g., Rathburn & Corliss 1994, Ernst & van der Zwaan 2004).

All these observations were summarized in the "TROX-model" of Jorissen et al. (1995), which relates the microhabitat "selection" of a given taxa to a balance between food and oxygen availability. According to this model, oligotrophic systems are food-limited and organisms are concentrated close to the sediment surface, where the majority of the food is located. Although eutrophic systems are oxygen-limited, organisms are also concentrated near the surface in order to avoid anoxic conditions deeper in the sediment. This general scheme has been refined by Jorissen (1999), van der Zwaan et al. (1999), and Fontanier et al. (2002) who suggested that: (1) the organic matter flux is the main parameter controlling foraminiferal microhabitats, (2) oxygen is not the limiting factor for deep infaunal species, and that (3) biological interactions, particularly competition for labile food material, may play a role in microhabitat selection.

Oxygen minimum zones (OMZs) are significant midwater features in the eastern Pacific Ocean (e.g., Helly & Levin 2004). It has been shown that, where the OMZ intercepts the continental margin, strong gradients are formed in both bottom water dissolved oxygen concentrations and organic matter input (Levin

et al. 2000). These gradients influence the biogeochemical properties of the underlying sediments and the distribution of benthic organisms within the sedimentary column. Usually organic-rich, oxygen-poor environments are dominated by meiofauna, mainly calcareous foraminifera and nematodes (e.g., Levin et al. 2002). In the last decades, significant advances have been made in the understanding of ecological aspects of benthic foraminifera from oxygen deficient settings in the world (see Bernhard & Sen Gupta 1999 for a review), including off Peru in the eastern south Pacific (Phleger & Soutar 1973, Levin et al. 2002).

Substantial progress in the knowledge of modern benthic foraminifera from the Chilean continental margin has been made since the early works of Bandy & Rodolfo (1964), Boltovskoy & Theyer (1970), and Ingle et al. (1980). More recent studies (e.g., Zapata & Moyano 1997, Figueroa et al. 2005, 2006, Hromic et al. 2006) have focused on taxonomic and/or biogeographical aspects, emphasizing the identification and characterization of zoogeographic provinces along the Chilean coast. But none of these studies investigated the relationship between living benthic foraminiferal fauna and environmental characteristics.

To provide new insight into benthic foraminiferal ecology off Concepción, Chile (~36° S), we present results on total and living benthic foraminifera from a bathymetric transect (80, 120, 1,030 m water depth; Table 1, Fig. 1A) that includes stations within (stations 18 and 26) and below the OMZ (station 40). Our study focused on (1) onshore-offshore, and (2) vertical distribution of calcareous foraminiferal communities within the sedimentary column (upper 10 cm) with regard to bottom water oxygen content and organic matter availability.

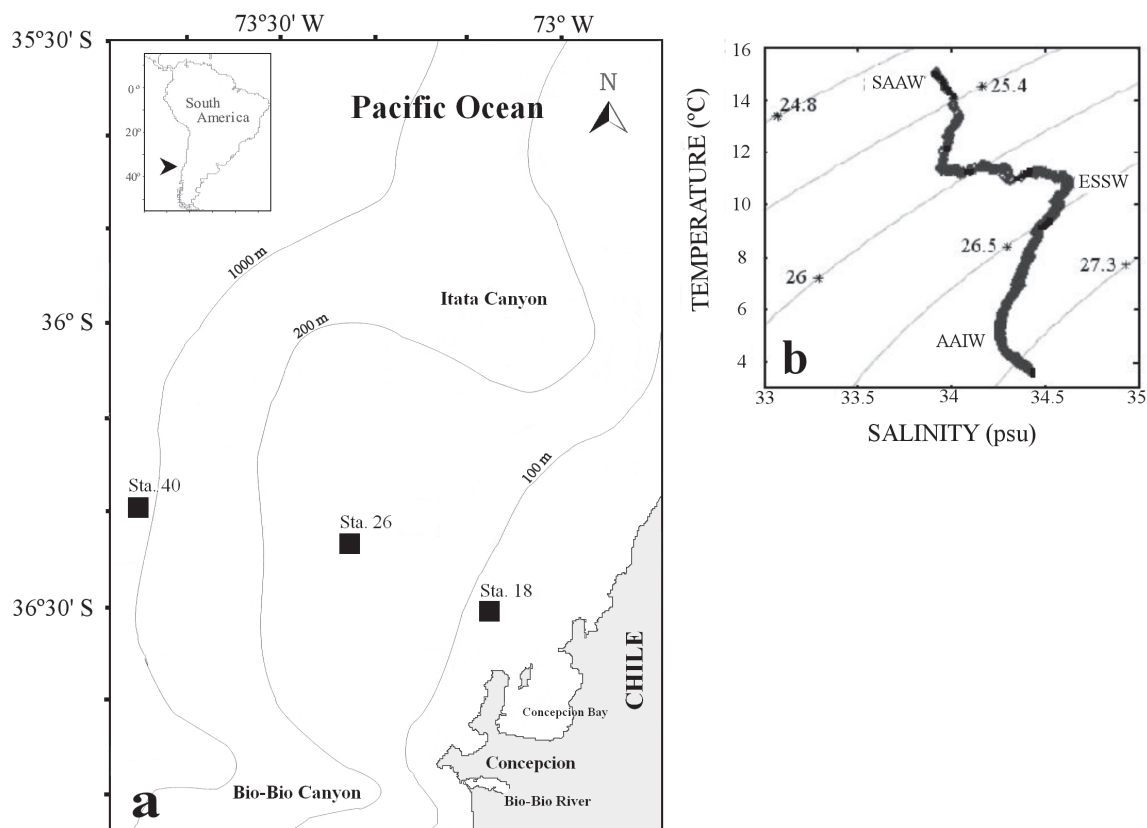
TABLE 1

## Location and collection date of sampling sites

Localización de las estaciones y fechas de muestreo

Station	Core	Collection date	Latitude (S)	Longitude (W)	Water depth (m)
18	MUC1803	12 August 2003	36°30'	73°07'	88
26	MUC2603	12 August 2003	36°26'	73°23'	120
40	RC4004	10 August 2004	36°20'	73°44'	1.030

MUC = Multicorer, RC = Rhumor corer



*Fig.1:* (A) Study area showing the position of the sampling stations off Concepción used in this study: station 18 (middle shelf), 26 (outer shelf), and 40 (on the middle slope), and bathymetry; (B) T-S diagram (April 2003) for station 40 showing the different water masses present: Subantarctic Water (SAAW), Equatorial Subsurface Water (ESSW), and Antarctic Intermediate Water (AAIW). See text for details.

(A) Área de estudio mostrando la posición de las estaciones de muestreo frente a Concepción utilizadas en este estudio: estaciones 18 (plataforma interior), 26 (plataforma exterior), y 40 (talud), y batimetría de la región; (B) diagrama T-S (abril 2003) para la estación 40 mostrando las diferentes masas de agua presentes: Agua Antártica Superficial (SAAW), Agua Ecuatorial Subsuperficial (ESSW) y Agua Intermedia Antártica (AAIW). Ver texto para detalles.

### Regional setting

The area off central-southern Chile has been studied in detail by various authors (Ahumada & Chuecas 1979, Sobarzo et al. 2001) including plankton variability, biogeochemical processes, and physical and chemical characteristics (Escribano & Schneider 2007).

Due to diverse factors (coastal winds, upwelling events, shelf width, and topographic settings), this area is one of the most productive sectors of the central-southern Chilean coast (35–45° S, Shaffer et al. 1999) with primary productivity values among the highest in the world ocean (Daneri et al. 2000, Schubert et al. 2000). Upwelling is strongly seasonal. It

intensifies during austral spring-summer, fertilizing the photic zone with the salty, nutrient-rich, oxygen-poor waters of the Equatorial Subsurface Water mass (ESSW) (Ahumada & Chuecas 1979). Upwelled ESSW can be found over the continental shelf and sometimes even at the inner part of Concepción Bay. Downwelling usually occurs in winter due to the prevalence of strong northerly winds (Sobarzo 1993).

High phytoplankton biomass and primary production (reaching 19.9 g C m<sup>-2</sup> d<sup>-1</sup>, Daneri et al. 2000) followed by high rates of organic matter sedimentation to the seafloor (e.g., Gutiérrez et al. 2000) promote anoxic/dysoxic conditions in the sediments (Neira et al. 2001).

Total organic carbon content (TOC) in the sediment is usually high and varies between 2 and 5 % (Table 2), with maximum TOC values in austral summer (Muñoz et al. 2007). Organic matter is mainly of phytoplanktonic origin (Schubert et al. 2000). Chlorophyll-*a* (Chl-*a*) concentrations in the surface sediments clearly decrease offshore (Table 2). On a yearly basis, C/N molar values fluctuate between 8.4 and 11.3 (Muñoz et al. 2007). Modern sedimentation rates are high (0.09-0.25 cm yr<sup>-1</sup>, Muñoz et al. 2004). Sediments are usually composed of silt and clay minerals with a mean grain size of 8.5-13.0 μm (Molina et al. 2004).

The study area is located on the widest portion of the continental margin off central-southern Chile (50 km) (Fig. 1A). The shelf is limited by two submarine canyons and their corresponding rivers: the Itata canyon (Itata River) to the north and the Biobío canyon (Biobío River) to the south. In general, three different water masses can be observed here: Subantarctic Water (SAAW) between the surface and about 80 m depth, ESSW at about 80 to 400 m with minimum dissolved oxygen concentrations, and Antarctic Intermediate Water (AAIW) below 400 m (Molina et al. 2004) impinging on the continental slope (Fig. 1B). The OMZ is associated with oxygen-depleted ESSW and intensifies by the local biogeochemical O<sub>2</sub> consumption (Paulmier et al. 2006). Off Concepción, the OMZ is less intense and its upper boundaries are deeper (about 100 m) than off northern Chile (Pizarro et al. 2002); its strength and the depth of the upper boundary vary seasonally. The OMZ's upper boundary is shallow in spring-summer (at 20 m from October to March) during the high upwelling activity period with O<sub>2</sub> concentrations lower than 0.2 mL<sup>-1</sup>, but it deepens in autumn (about 50 m in April-May) (Paulmier et al. 2006).

#### MATERIAL AND METHODS

The sediment samples used in this study were collected during winter cruises as part of the COPAS Center Time Series Study off Concepción (Table 1). A SMBA-type multi-corer (MUC) with six sampling tubes (inner diameter = 9.5 cm) was used for sampling at Sta. 18 (middle shelf, 88 m water

depth) and 26 (outer shelf, 120 m water depth) (Fig. 1A). A Rhumor corer (RC) - a type of gravity corer that recovers the sediment-water interface - was used at Sta. 40 (middle slope, 1,030 m water depth). The RC uses an acrylic of 7 cm internal diameter and ~ 100 cm in length. One core tube was analyzed for each station. Due to the limited data set, interannual and seasonal changes cannot be addressed.

The cores were sliced at 0.5 cm intervals for the upper 2-3 cm, and every 1 cm downcore. Immediately after slicing, the samples were preserved and stained according to the methodology of Rathburn & Corliss (1994); samples were allowed to stain for at least one week before processing for foraminifera analysis. Samples were not split but examined entirely for their content of live foraminifera. The use of Rose Bengal stained foraminifera to interpret living associations was critically discussed by Bernhard (1988). One problem of this technique is the fact that Rose Bengal may stain the protoplasm of dead foraminifera, which may be relatively well preserved under anoxic conditions leading to an overestimation of the living fauna. However, it is still the most frequently used method in foraminifera research and the most practical one (Bernhard 2000). Our definition of "stained" (living) foraminifera was very strict and only specimens with all chambers, except for the last one (the youngest) stained bright pink were counted as stained.

After staining, samples were wet-sieved using 63, 180, and 250 μm mesh-opening. The data presented here are from the > 250 and 180-250 μm fractions and refer to the upper 10 cm of each core. The mesh sizes were selected in keeping with the methodology previously used for the COPAS Time Series Study off Concepción (Tapia 2003). The fraction 63-180 μm was preserved for future studies.

We are aware of the fact that the selection of the > 180 μm size fraction may have introduced some bias regarding the abundance of total foraminifers as well as the abundance of smaller organisms. Although the smaller size fraction (e.g., 63-150 μm) may contain a large number of foraminiferal species and juvenile forms that are rare or absent in the larger size fraction (e.g., Schröder et al. 1987), their removal is extremely time-consuming. Additionally, smaller specimens are often more problematic to identify to the species level.

TABLE 2

## Summary of available water column and surface sediment characteristics off Concepción

Resumen de la características de la columna de agua y sedimentos para el área frente a Concepción

Water column	Station					
	18(88 m)		26(120 m)		40(1,030 m)	
	Summer	Winter	Summer	Winter	Summer	Winter
Bottom water dissolved oxygen (mL <sup>-1</sup> )	0.07 <sup>1</sup>	0.45 <sup>1</sup> (0.17) <sup>a</sup>	0.4 <sup>2</sup>	0.6 <sup>2</sup>	3.4 <sup>1</sup>	2.9 <sup>1</sup> (2.7) <sup>b</sup>
Surface water temperature (°C)	13.3 <sup>1</sup>	12.5 <sup>1</sup> (11.8) <sup>a</sup>	nd	14.6 <sup>1</sup>	12.3 <sup>1</sup>	
Bottom water temperature (°C)	10.5 <sup>1</sup>	10.8 <sup>1</sup> (11.2) <sup>a</sup>	9.2 <sup>2</sup>	11.6 <sup>2</sup>	4.6 <sup>1</sup>	4.0 <sup>1</sup>
Surface water salinity (psu)	32.2 <sup>1</sup>	32.9 <sup>1</sup> (32.8) <sup>a</sup>	nd	33.8 <sup>1</sup>	34.7 <sup>1</sup>	
Bottom water salinity (psu)	34.6 <sup>1</sup>	34.5 <sup>1</sup> (34.6) <sup>a</sup>	35.9 <sup>2</sup>	35.1 <sup>2</sup>	34.2 <sup>1</sup>	34.3 <sup>1</sup>
Sediments	Middle shelf		Outer shelf		Middle slope	
Chlorophyll- <i>a</i> (µg g <sup>-1</sup> ) *	24.1 <sup>3</sup>	21.9 <sup>3</sup> (8.1) <sup>3</sup>	28.7 <sup>2</sup>	27.9 <sup>2</sup>	13.4 <sup>4</sup>	nd
% TOC *	3.9 <sup>3</sup>	3.3 <sup>2</sup>	4.6 <sup>2</sup>	5.1 <sup>2</sup>	2.9 <sup>5</sup>	2.1 <sup>4</sup>
Eh (mV) *	120 <sup>2</sup>	168 <sup>2</sup>	176 <sup>2</sup>	139 <sup>2</sup>	257 <sup>4</sup>	nd

Sources: <sup>1</sup>CTDO data (2002-2004) (<http://copas.udec.cl/eng/research/timeseries.php>) from COPAS Time-Series off Concepción averaged for summer and winter seasons; <sup>2</sup>Gutiérrez (2000), includes data within the El Niño 1997-98 period; <sup>3</sup>Muñoz et al. (2007); <sup>4</sup>Gallardo et al. (2004); <sup>5</sup>Böning et al. (2005). Data in parentheses refer to the sampling time of this study, based on CTDO profiles (<sup>a</sup>) or Niskin bottles (<sup>b</sup>); (\*) data for the first centimeter of sediment; nd = no data available. Bottom water oxygen and temperature measured at 80 m depth at station 18, and at 750 m depth at Station 40

To our knowledge, there is only one quantitative (unpublished) study of living benthic foraminifera available for the shelf off Concepción (Mayor et al. unpublished results). Our results may have underestimated the total number of living foraminifera in the study area (shelf stations) by ca. 20 % as compared with the abundances obtained by Mayor et al. (unpublished results) for the > 150 µm fraction. However, the total numbers of benthic foraminifera (stained + dead) and species that we found for the slope area off Concepción falls within the range obtained by Figueroa et al. (2005, 2006) who analyzed the > 150 µm at nearby slope and deep stations. An important aspect is that a scan of the > 63 µm fraction revealed that, with the exception of tiny *Globobulimina* and *Stanforthia*, the overall species composition for the Concepción area is comparable in both small and coarser size fractions.

The total density of living calcareous foraminifera was determined by integrating the numbers of live individuals picked at all levels from 0 to 10 cm sediment depth. Percentages of individual taxa were calculated from the raw density data. Concerning vertical profiles,

foraminiferal densities were normalized to 50 cm<sup>3</sup> sediment volume for each 0.5 and 1 cm layer. Finally, with the purpose of comparison with other areas, living calcareous foraminifera were normalized to 50 cm<sup>2</sup> for the first centimeter.

We assigned the benthic foraminifera to two different microhabitat groups (shallow and deep infauna). None of the species off Concepción could be considered to be strictly epifauna as defined by Buzas et al. (1993) who suggested that only species living on elevated substrates can be assigned to this category.

In order to provide an overview of the environmental characteristics in the study area, we present available water column and surface sediment data in Table 2; in those cases when environmental data were not available for the dates we collected the cores, we resorted to previously published data. Water column data derive mostly from the COPAS Time Series Study off Concepción (<http://copas.udec.cl/eng/research/timeseries.php>), and include CTDO data (2002-2004) and/or data obtained from Niskin bottles (station 40). The sediment data stem from several sources (Gutiérrez 2000, Gallardo et al. 2004, Muñoz et al. 2007).

## RESULTS

The sediments off Concepción were typically greenish-brown in color (7.5 Y 3/2-7.5 Y 4/2 Munsell table color). Fecal pellets were numerous at the shallower stations (Sta. 18 and 26). A grey layer of very fine material was observed at 7-9 cm depth in the core from station 40. Available Chl- $\alpha$  and TOC data (although not always coincident with our August samplings) reveal that the sediments of the shelf stations are generally characterized by higher levels of Chl-*a* concentrations and TOC ( $> 20 \mu\text{g g}^{-1}$  and  $> 3.3 \%$ , respectively) than the slope station 40 (Table 2). Bottom water dissolved oxygen (BWDO) conditions differed along the transect. Minimum BWDO values ( $0.17 \text{ mL}^{-1}$ ) were encountered at station 18 (88 m water depth) and maximum values at station 40 ( $2.7 \text{ mL}^{-1}$ ) during our August samplings (Table 2), in agreement with known OMZ boundaries in the area. Redox potential values at the sediment surface (Eh) agree with increasing bottom water dissolved oxygen concentrations from onshore to offshore (Table 2).

Using the BWDO values given in Table 2, the stations could be grouped into two

categories according to Sen Gupta & Machain-Castillo (1993) classification of environments: (1) shelf stations 18 and 26, with dysoxic-suboxic conditions ( $< 2 \text{ mL}^{-1}$ ), located at and immediately below the upper boundary of the OMZ, respectively; and (2) slope station 40, with oxygenated conditions ( $> 2 \text{ mL}^{-1}$ ), located several hundred meters below the OMZ. Bottom water temperature, salinity, and BWDO (Table 2) showed the influence of the ESSW at Sta. 18 and 26, whereas AAIW affected Sta. 40.

#### *Onshore-offshore distribution of benthic foraminifera*

The analysis of benthic foraminifera in the cores off Concepción showed that the contribution of the  $> 250 \mu\text{m}$  fraction to the total fauna (larger than  $180 \mu\text{m}$ ) increased offshore (Table 3) from 1.8 % (88 m) to 16 % (120 m) and 29 % (1030 m water depth).

At all three stations, rotalid foraminifera were the main component of the total benthic foraminiferal fauna ( $> 75 \%$ ). Agglutinated foraminifera were very rare (0.4 %) at Sta. 18 but reached 8 and 16 % of the total fauna at station 26 and 40, respectively. Miliolids were only present at station 40 ( $\sim 1 \%$ ) (Table 3).

TABLE 3

Size range of benthic foraminifera, relative abundance of the three main groups (Agglutinated, Rotalid and Miliolid in the  $> 180 \mu\text{m}$  fraction), total number of living species, percentage of living calcareous foraminifera with respect to total benthic foraminifera, and total benthic foraminifera ( $> 180 \mu\text{m}$ , calcareous + agglutinated) within the upper 10 cm of each core at stations 18, 26 and 40. Totals are standardized to  $50 \text{ cm}^2$  surface area and 10 cm sediment depth

Rango de tamaño de los foraminíferos bentónicos, abundancia relativa de los tres principales grupos (Aglutinados, Rotalidos y Miliolidos en la fracción  $> 180 \mu\text{m}$ ), número de especies vivas, porcentaje de foraminíferos bentónicos calcáreos vivos con respecto al total de bentónicos, y foraminíferos bentónicos totales ( $> 180 \mu\text{m}$ , calcáreos + aglutinados) dentro de los primeros 10 cm de cada testigo de sedimento para las estaciones 18, 26 y 40. Los totales están estandarizados a  $50 \text{ cm}^2$  de superficie y 10 cm de profundidad de sedimento

Characteristic		Station 18(88 m)	Station 26(120 m)	Station 40(1,030 m)
Size range	$> 250 \mu\text{m}$ (%)	1.8	16	29
	250-180 $\mu\text{m}$ (%)	98.2	84	62
Main groups	Rotalid foraminifera (%)	99.6	92	83
	Agglutinated foraminifera (%)	0.4	8	16
	Miliolid foraminifera (%)	0	0	$\sim 1$
	Total number of living species	3	10	18
Percentage of living	Living calcareous foraminifera (%)	60	18	7
	Total benthic foraminifera	615	1,904	5,252

Table 4 provides the listing of all living benthic foraminifera species found in this study. Stations 18 and 26 shared the same live calcareous assemblage. Both stations were characterized by the dominance of *Nonionella auris* (d'Orbigny), which made up > 90 % of the total fauna of stained calcareous foraminifera (Table 5). In contrast, foraminiferal live assemblage at station 40 strongly differed. Here, *Bolivina spissa* Cushman, *Globobulimina affinis* (d'Orbigny), *Chilostomella oolina* Schwager, and *Uvigerina peregrina* Cushman were the most relevant taxa (Table 5).

The relative abundance of stained calcareous foraminifera (> 180 µm, Table 3) as well as their densities within the first centimeter (Table 6) decreased drastically from shelf to slope (i.e., from 161-198 at shelf stations 18 and 26 to 96 specimens per 50 cm<sup>2</sup> at Sta. 40).

#### *Downcore pattern and microhabitat of benthic foraminifer species*

Stations 18 and 26 showed the highest concentrations of stained organisms near the

sediment surface (Fig. 2); indeed, 50 and 60 % (cumulative percent) of total living calcareous foraminifera were observed within the first centimeter at each station. In contrast, station 40 contained only 30 % of the total stained calcareous foraminifera at the surface, and a maximum was observed at 1-1.5 cm (~ 22 % of total living calcareous foraminifera) (Fig. 2). In addition, minor secondary abundance peaks were observed at station 18 and 40 between 5-6 cm (~ 5 %) and 3-4 cm (~ 9 %), respectively (Fig. 2).

Identification of species microhabitat was based on the presence or absence of an infaunal maximum, and on the shape of the distribution profile of each species (position with respect to other taxa; Fig. 3). Based on these assumptions, we defined the species *N. auris*, *B. spissa*, *U. peregrina*, *B. seminuda* and *B. costata* as shallow infauna, and *G. affinis* and *C. oolina* as deep infauna. The high abundance of shallow infauna and the absence of deep infauna characterized the shelf stations located under the OMZ's influence (station 18 and 26). In contrast, shallow and deep infaunal species were observed at the slope station 40 (1,030 m water depth).

TABLE 4

#### Living (stained) benthic foraminifers identified in this study

Foraminíferos bentónicos vivos (teñidos) identificados en este estudio

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<i>Bolivina costata</i> d'Orbigny, 1839.
<i>Bolivina plicata</i> d'Orbigny, 1839.
<i>Bolivina seminuda</i> Cushman = <i>Bolivina seminuda</i> var. <i>humilis</i> Cushman and McCulloch, 1942.
<i>Bolivina spissa</i> Cushman = <i>Bolivina subadvena</i> Chusman var. <i>spissa</i> Chusman, 1926.
<i>Bulimina denudata</i> Cushman and Parker, 1938.
<i>Cassidulina limbata</i> Cushman and Hughes 1925.
<i>Chilostomella oolina</i> Schwager 1878.
<i>Cibicidoides wuellerstorfi</i> (Schwager, 1866) = <i>Cibicidoides wuellerstorfi</i> Resig, 1981.
<i>Dentalina communis</i> (d'Orbigny) = <i>Nodosaria</i> ( <i>Dentalina</i> ) <i>communis</i> d'Orbigny, 1826.
<i>Epistominella pacifica</i> (Cushman) = <i>Pulvinulinella pacifica</i> Cushman, 1927.
<i>Gyrodinoides neosoldanii</i> (Brotzen) = <i>Gyroidina neosoldani</i> Ingle et al., 1980.
<i>Globobulimina affinis</i> (d'Orbigny) = <i>Bulimina affinis</i> d'Orbigny, 1839.
<i>Martinottiella communis</i> (d'Orbigny) = <i>Clavulina communis</i> d'Orbigny, 1826.
<i>Melonis barleeana</i> (Williamson) = <i>Nonionina barleeana</i> Williamson, 1858.
<i>Nonionella auris</i> (d'Orbigny) = <i>Valvulina auris</i> d'Orbigny, 1839.
<i>Pyrgo murrhina</i> (Schwager, 1866) = <i>Pyrgo murrhyna</i> Resig, 1981.
<i>Sacamina atlantica</i> (Cushman) = <i>Proteonina atlantica</i> Cushman, 1944.
<i>Uvigerina peregrina</i> Cushman, 1923.

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TABLE 5

Living benthic foraminiferal census data of the more representative taxa in the > 180  $\mu\text{m}$  fraction at Sta. 18, 26, and 40 (numbers are not standardized for a given sediment volume and refer to total organisms in each interval) within the upper 10 cm of the sediment column. Microhabitat (Mh) patterns are summarized as shallow infaunal (SI) or deep infaunal (DI) taxa

Censo de los taxa más representativos de foraminíferos bentónicos vivos en la fracción > 180  $\mu\text{m}$  presentes en las estaciones 18, 26 y 40 (los números no están estandarizados para un volumen de sedimento y se refieren al total de organismos en cada intervalo) dentro de los primeros 10 cm de la columna de sedimento. Los microhábitat (Mh) están agrupados en taxa de infauna somera (SI) o infauna profunda (DI)

Station	0-0.5 cm	0.5-1 cm	1-1.5 cm	1.5-2 cm	2-3 cm	3-4 cm	4-5 cm	5-6 cm	6-7 cm	7-8 cm	8-9 cm	9-10 cm	Total number living forams	Mh	Percentage of total calcareous living fauna
Station 18	136	89	83	72	41	22	9	37	17	3	5	4	518	SI	99
<i>N. auris</i>															
Others	4	0	0	0	0	0	1	0	0	0	0	0	5		1
Station 26															
<i>N. auris</i>	140	115	115	39	17	8	7	3	1	3	1	0	449	SI	92.8
<i>B. seminuda</i>	2	10	2	1	0	0	0	0	0	0	0	0	15	SI	3.1
<i>B. costata</i>	4	2	1	1	0	0	0	0	0	0	0	0	8	SI	1.6
Others	4	2	3	2	1	0	0	0	0	0	0	0	12		2.5
Station 40															
<i>B. spissa</i>	31	26	49	18	4	3	17	1	8	4	0	1	162	SI	57.5
<i>G. affinis</i>	2	3	4	2	7	9	14	7	2	8	1	2	61	DI	21.6
<i>C. oolina</i>	4	4	0	1	4	2	8	4	4	2	0	0	33	DI	11.7
<i>U. peregrina</i>	1	2	1	3	1	0	0	0	0	0	0	0	8	SI	2.8
Others	1	0	1	5	2	1	8	0	0	0	0	0	18		6.4



TABLE 6

Number of species and density data for living (stained) benthic foraminifera from low-oxygen environments (modified from Gooday 2003), compared to our study area. ND = no data

Número de especies y densidad de foraminíferos bentónicos vivos (teñidos) de ambientes pobres en oxígeno (modificado de Gooday 2003) comparados con nuestra área de estudio. ND = sin datos

Site and depth	BWDO (mL <sup>-1</sup> )	Number of species	Stained specimens per 50 cm <sup>2</sup>	Reference; size fraction and horizon examined
Oman margin				Gooday et al. (2000)> 63 µm, 0-1 cm
412 m	0.13	64	65,535	
3,350 m	~ 3.00	208	2,930	
Santa Barbara basin				Phleger & Soutar (1973)> 62 µm, surface sediment
575 m	~ 0.1	~ 13	5,875	
590 m	~ 0.1	ND	5,250	
Santa Barbara basin				Bernhard (1990)> 63 µm, 0-1 cm
486 m (Feb 1988)	~ 0.11	ND	2,660	
550 m (June 1988)	< 0.1	ND	34,505	
550 m (Feb 1988)	< 0.1	ND	21,700	
550 m (June 1988)	< 0.1	ND	47,785	
550 m (Oct 1988)	0.01	ND	48,130	
550 m (July 1989)	Anoxic	ND	135	
Santa Barbara basin				Bernhard et al. (1997)> 63 µm, 0-1 cm
339 m	0.51	7	2,660	
431 m	0.35	11	34,505	
522 m	0.08	10	9,430	
537 m	0.04	12	6,350	
591 m	0.06	9	19,790	
Point Concepcion				Shepperd et al. (2007)> 150 µm, 0-1 cm
990 m (May 1996)	0.47	3	188	
990 m (Aug 1996)	0.46	3	308	
990 m (Oct 1996)	0.44	7	246	
Callao (Perú)				Phleger & Soutar (1973)> 62 µm, surface sediment
180 m	ND	~ 11	~ 3,000	
Callao (Perú)				Levin et al. (2002)> 150 µm, 0-1 cm
305 m	0.02	ND	29,043	
563 m	0.26	ND	926	
831 m	0.84	ND	497	
1,211 m	1.78	ND	96	
Concepción (Chile)				This study> 180 µm, 0-1 cm
88 m (August 2003)	~ 0.2	3	161	
120 m (August 2003)	ND	10	198	
1030 m (August 2004)	> 2	18	96	

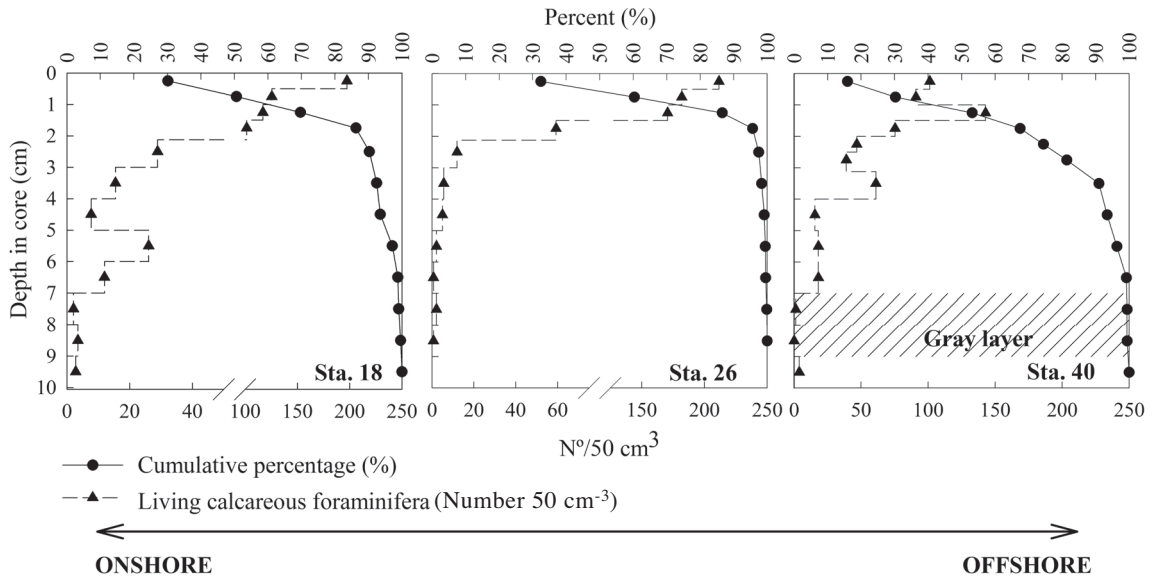


Fig.2: Vertical distribution of total living benthic calcareous foraminifera (Rose Bengal stained, fraction > 180  $\mu\text{m}$ , standardized to 50  $\text{cm}^3$  sediment volume), and cumulative percent of living organisms within the upper 10 cm of each core.

Distribución vertical de los foraminíferos calcáreos vivos totales (teñidos con Rosa de Bengala, fracción > 180  $\mu\text{m}$ , estandarizados a 50  $\text{cm}^3$  de sedimento) y porcentaje acumulado de organismos vivos dentro de los primeros 10 cm de cada testigo de sedimento.

#### DISCUSSION AND CONCLUSIONS

We are aware that the conclusions we can draw from our study are limited by the reduced sampling occasions and by the size fraction selected (> 180  $\mu\text{m}$ ), which may have introduced some bias regarding to the abundance of total foraminifera. Nevertheless, these data provide valuable insights into the ecology of foraminifera in the region and the trends indicated by our foraminiferal data may serve as groundwork for future testing.

Despite the methodological differences, our 0-1 cm density data of stained specimens (standardized to 50  $\text{cm}^2$ ) are comparable to the values observed off Point Conception, California, by Shepperd et al. (2007) and suboxic slope settings off Callao, Peru, by Levin et al. (2002), who used size fractions > 150  $\mu\text{m}$  (Table 6). Our data are lower than those reported for the oxygen-poor Santa Barbara Basin (Bernhard 1990, 1992) and much lower than the Arabian Sea, where densities of tens of thousands of living benthic foraminifera (fractions > 63 and 150  $\mu\text{m}$ ) have been found in

surface sediments influenced by low oxygen conditions (Gooday et al. 2000) (Table 6).

According to Sen Gupta & Machain-Castillo (1993), about ten calcareous foraminifer species typically live in oxygen-poor areas, with two or three species usually comprising as much as 80 % of the fauna. In our study, the number of living calcareous species for shelf stations 18 and 26 varied between 3 and 10 (Table 3 and 6); ~ 90 % of the total calcareous living benthic foraminiferal fauna were composed by one species (Table 5). The number of species is similar to that found in the Santa Barbara basin, California, by Phleger & Soutar (1973) and Bernhard et al. (1997), who reported 7-13 stained species of calcareous foraminifera in the > 63  $\mu\text{m}$  fraction (Table 6), and to Peru, where one species (*Bolivina cf. pacifica*) composes > 95 % of the living fauna (Phleger & Soutar 1973). In contrast, our data are much lower than those reported for the Oman Margin, where the total number of stained species observed by Gooday et al. (2000) varied between 49 (> 125  $\mu\text{m}$ ) and 64 (> 63  $\mu\text{m}$ ).

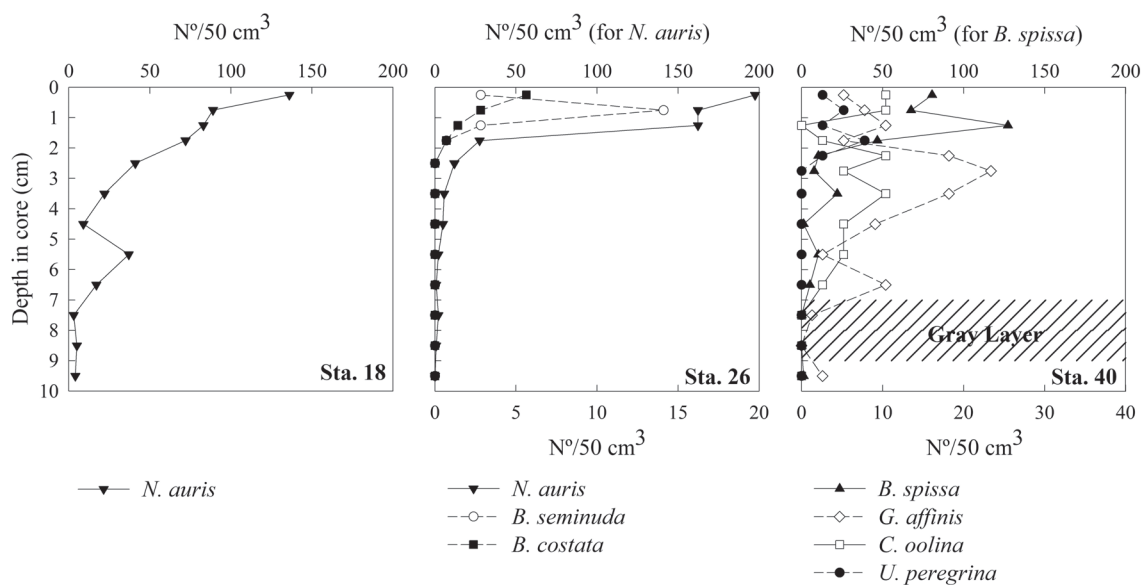


Fig.3: Vertical distribution of the most important taxa of living benthic calcareous foraminifera (Rose Bengal stained, fraction > 180  $\mu\text{m}$ , standardized to 50  $\text{cm}^3$  sediment volume) within the upper 10 cm of each core.

Distribución vertical de las especies de foraminíferos calcáreos vivos más importantes (teñidos con Rosa de Bengala, fracción > 180  $\mu\text{m}$ , estandarizados a 50  $\text{cm}^3$  de sedimento) dentro de los primeros 10 cm de cada testigo de sedimento.

#### Onshore-offshore distribution of living foraminifera

It is well known that benthic foraminiferal abundances in marine sediments are closely related to food availability, and foraminifera generally prosper where food is abundant (Gooday et al. 2000). Along our transect, we detected a decreasing trend in living foraminifera (> 180  $\mu\text{m}$ ) within the first centimeter with increasing water depth (from 161-198 at stations 18 and 26 to 96 specimens per 50  $\text{cm}^2$  at station 40, Table 6). This is most probably induced by lower and less labile organic matter flux reaching the sea floor in deeper settings such as those of Sta. 40 (Schubert et al. 2000, Molina et al. 2004, Muñoz et al. 2004), and/or a reduction in predation pressure at oxygen-depleted settings such as stations 18 and 26 (Gooday 2003). Although available Chl- $\alpha$  and TOC measurements do not coincide with the sampling times for foraminifera, on hand data show that station 40 is generally characterized by lower levels of Chl- $\alpha$  concentrations and TOC (~ 13  $\text{mg g}^{-1}$  and < 3 %, respectively) than the shelf stations (Table 2).

In order to gain access to food, benthic foraminifera must tolerate the oxygen depletion that frequently accompanies abundant organic matter. Reduced oxygen concentrations and/or recurring anoxia events will influence the size distribution and taxonomic composition of foraminiferal assemblages, eliminating the less tolerant species, whereas abundance and dominance increase for the remaining species (Sen Gupta & Machain-Castillo 1993, Gooday et al. 2000). Our observations are consistent with these concepts, showing minimal presence of large foraminifera and the dominance of a low diversity assemblage in the oxygen-poor conditions of the shallowest stations (18 and 26), which are associated with the upper boundary of the OMZ. Here, the shelf restricted *N. auris* (Resig 1981) (in fraction > 180  $\mu\text{m}$ , Table 5) composed over 90 % of the total living calcareous foraminifera fauna. A quick scan of the > 63  $\mu\text{m}$  fraction revealed that *N. auris* was dominant (data not shown) at these shelf stations and was accompanied by juvenile bolivinids (about 30 %) at station 26.

The dominance of *N. auris* at the two stations associated with the OMZ differs from

observations by Ingle et al. (1980), who found typical OMZ foraminiferal fauna (> 250  $\mu\text{m}$  fraction) in central Chile to be primarily composed by bolivinids such as *Bolivina seminuda* and *Bolivina costata*. Bolivinids had a minimal presence or were absent in the 180  $\mu\text{m}$  fraction at Sta. 18 and 26 and, as stated above, juveniles were only observed in the > 63  $\mu\text{m}$  fraction at station 26. The discrepancy between our data and those of Ingle et al. (1980) may be explained by the fact that bolivinids are commonly associated with stable OMZ conditions (Heinze & Wefer 1992), which is not the case for our study area with a seasonally variable OMZ (Paulmier et al. 2006). In contrast, the living assemblage observed at station 40 (dominated by *B. spissa*, *G. affinis*, *U. peregrina*, *C. oolina*) agrees with the one reported previously by Ingle et al. (1980) at similar water depths.

*Vertical distribution of living foraminiferal fauna within the upper sediment column (10 cm)*

The relationship of the benthic foraminiferal microhabitat with food availability and oxygenation of the benthic realm has been schematized in a conceptual model by Jorissen et al. (1995). The TROX-model explains that, in oligotrophic environments, species adapted to low organic flux conditions will thrive close to the sediment-water interface in a well-oxygenated setting. The low flux of organic matter to the sediment prevents colonization of the deeper sediment layers by infaunal taxa. In eutrophic conditions, on the other hand, where the principal redox front is positioned close to the sediment surface, infaunal taxa are limited to the first millimeters or centimeters of the sediment (Murray 2001); in this case, they have only a limited tolerance for low oxygen conditions.

Faunal penetration is maximal in "mesotrophic" settings because the oxygen penetration is relatively deep and more or less labile food particles are introduced at depth in the sediment by bioturbating macrofauna creating suitable microhabitats for benthic foraminifera (Jorissen 1999, Fontanier et al. 2002). In such environments, the subsurface accumulation of organic matter (Rathburn & Corliss 1994) and/or grazing on populations of anaerobic bacteria associated with redox

boundaries (Fontanier et al. 2002) could explain the microhabitat selection of a given foraminifer.

In general terms, the vertical patterns observed at our stations agree with the TROX-model. At stations 18 and 26, the living foraminifera are located preferentially near the sediment surface (50 and 60 % of the total living foraminifera within the first centimeter, Fig. 2). Particularly, species tolerant to low oxygen conditions with shallow infaunal microhabitat preferences (Bernhard & Sen Gupta 1999) at stations 18 and 26 indicate eutrophic conditions. On the other hand, the deepest penetration of foraminiferal fauna at station 40 is more typical of mesotrophic conditions (70 % of total living calcareous foraminifera occur below the first centimeter). Here, an important proportion of the living population is composed of deep infaunal species such as *G. affinis* (~ 22 %) and *C. oolina* (~ 12 %) (Table 5). This general scenario would suggest that BWDO is the main controlling agent at stations 18 and 26, whereas food supply controls the distribution of benthic foraminifera at station 40.

The extensive vertical distribution of *N. auris* at station 18, even with a small peak of stained organisms in the 5-6 cm level (Fig. 2), is interesting to note. This feature may have two explanations. On the one hand, it could refer to an artifact of the Rose Bengal method which may have stained the protoplasm of dead foraminifera (Material and Methods section) at this shallow station. On the other hand, it may be explained by the strong seasonal variation in bioturbation affecting the upper 2-5 cm of the sediment column associated with highly seasonally variable BWDO concentrations and organic matter supply (Muñoz et al. 2007, Table 2). In fact,  $^{210}\text{Pb}$  activity profiles show an average mixed layer depth of 5 cm at station 18 (Muñoz et al. 2007). An additional factor to the pattern observed at station 18 could include the denitrification capabilities of *N. cf. stella* (most probably *N. auris*, according to published photographs, Risgaard-Petersen et al. 2006) which, although pushed deeper down the sedimentary column by bioturbation, would allow them to remain alive.

In summary, our results show that a clear difference exists between shelf stations 18 and 26 which are dominated mostly by one species tolerant to oxygen depletion, and slope station

40 where oxygen availability and food introduction within the sediment allow the occurrence of shallow and deep infaunal species.

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