



Distribution and paleoecology of molluscan skeletal remains along an upwelling tract: Benguela system, Namibian shelf



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ABSTRACT

This study describes and categorizes the preservable, and thus predominantly molluscan, component of the macrofauna death assemblages of sub-environments within the northern Benguela upwelling system. This is especially important for assembling actualistic data that can later serve for identifying similar settings in the geological record.

A total of 16 samples were examined. Contrary to stereotypes, benthic communities are present but highly variable across the high-productivity tract and are characterized by distinctive community structures. Benguela system document a decrease in body size of chemosymbiotic bivalves (lucinids) and percent of chemosymbionts and deposit-feeders, and an overall increase in species richness and epifaunal-infaunal ratio. This trend is in accordance with the upwelling facies-gradient from diatomaceous ooze in areas of maximum upwelling intensity outward to the aerated but food-abundant carbonate oozes and spatially coexisting phosphorite concentrations. Differences in seafloor oxygen concentration along with variable food availability played major roles in structuring the death assemblages under the Benguela upwelling system.

The ecologic data provide ways to distinguish between facies of low and high shell production along an increasing oxygen gradient, and also between assemblages with moderate and higher species richness associated with time-averaging. The data support the existence of a wider range of time averaging in the formation of molluscan sand and gravel samples in the northern Benguela than previously appreciated.

Given the scarcity of information on macrobenthic ecology from modern high-productivity settings, these death assemblages can represent a "modern" analog.

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1. Introduction

The Benguela current is one of the world's four major eastern boundary current systems. Off the coast of southwest Africa an intensive wind-induced coastal upwelling persists (Hutchings et al., 2009). In response to nutrient enrichment from deeper waters, the surface waters hold high abundances of diatoms (Schuette and Schrader, 1981) that, after death, settle to the seafloor, generating one of the most organic-rich sediments in today's oceans, up to 24.6% C_{org} by weight (Bremner, 1978, 1983; Shannon, 1985; Rogers and Bremner, 1991). The continental shelf off Namibia is also one of the deepest and widest shelves in the world (Bremner, 1981) and is characterized by sediments rich in silica, organic matter and phosphate. The Benguela upwelling system has been the subject of a great deal of investigation regarding its physical oceanography (e.g., Shannon, 1985), chemical oceanography (e.g., Chapman and Shannon, 1985) and geochemistry (e.g., Calvert and Price, 1983). A detailed review of the marine geological aspects of the underlying sediments was given by Rogers and Bremner (1991). They reported "molluscan sand and gravel" as a significant component of

carbonate oozes on the Walvis middle shelf (up to 50% weight; Bremner, 1983; Rogers and Bremner, 1991), especially in some samples shoreward of the 200 meter isobath. However, they reportedly rarely comprised an important component of the shelf sediments (Bremner, 1983; Rogers and Bremner, 1991). General biodiversity patterns of these upwelling deposits have been studied, and some molluscan fauna identified (Sakko, 1998; Zettler et al., 2009). However, many of these studies have been based on only a few or single localities, and thus, many questions regarding the environmental deposition of the upwelling seafloor remain unanswered, especially variations across the full breadth of the upwelling facies belt including the continental shelf itself.

The low-oxygen conditions that characterize these systems bring the assumption that they hold very low benthic invertebrate abundances and diversity. However, ecological studies in other regions of low oxygen and/or high organic-matter show that these kinds of settings are not devoid of macrofauna, but rather that the macrobenthic communities are highly variable. Distinct environmental gradients in the structure of macrobenthic communities (e.g., species richness, abundance, composition, burrow diameter size) can typically be found across such areas (e.g., Rhoads and Morse, 1971; Savrda et al., 1984;

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Arntz et al., 1991; Stachowitsch, 1991; Tyson and Pearson, 1991; Clarke and Warwick, 1994; Levin et al., 2000; Zettler et al., 2009, 2013).

Ecological information can be inferred from the morphology and taxonomic composition of macrobenthic death assemblages. Quantitative tests of “live–dead agreement” in modern environments indicate that molluscan skeletal death assemblages capture the composition and community structure of the local living community to a high degree (Aller, 1995; Kidwell, 2001, 2002), matching or even exceeding the quality of information acquired from any single biological census, due to the summing of seasonal and annual variations in time-averaged death assemblages (see review by Kidwell, 2013). In this way, ecological characterizations based on macrobenthic death assemblages can be considered as a more complete “modern” picture than information based on live censuses alone, and are particularly appropriate for comparisons with possible ancient analogs (where fossil assemblages are probably also time-averaged).

This study investigates the paleoecological significance of macrobenthic invertebrate death assemblages accumulated under upwelling conditions. Specifically, it explores macrobenthic evidence for bottom-water conditions across the Benguela upwelling system off the Namibian coast, and the role of bottom oxygen levels and/or organic matter concentrations in shaping the benthic system. This is the area of Brongersma-Sanders' (1957) classic work on the role of upwelling in mass mortalities in the sea, making it a particularly interesting shelf for ecological evaluation of shelled benthos. Contrary to stereotypes, benthic community structure is highly variable across the high-productivity tract.

2. Oceanographic settings

Within the Atlantic continental shelf of Namibia, the Walvis Shelf is relatively wide (~140 km to the shelf-break), with both an inner and an outer shelf break at ~200 and ~400 m water depth, respectively (Shannon, 1985; Longhurst, 1998). The Walvis shelf is part of a passive margin, contrasting with the other well-studied modern upwelling areas of Peru, Baja California, and the southern California borderlands.

The modern Walvis shelf comprises a classic suite of high-productivity lithotypes (Rogers and Bremner, 1991). The inner shelf is a mosaic of diatomaceous ooze and organic-rich muds, and the remainder of the shelf and upper slope are dominated by foraminiferal ooze and patches of phosphorite that contain >20% phosphorite grains by weight (Fig. 1). However, phosphorite is a variable but subsidiary component (usually <20%) of all lithologies. Phosphorite-rich patches on the inner shelf are thought to be relict deposits from previous sea level lowstands (Bremner, 1978, 1983). However, the landward flank of the inner belt of diatomaceous ooze is one of the few sites in the world where concretionary phosphorites are presently forming (Baturin, 1982; Rogers and Bremner, 1991).

The Walvis Shelf has experienced upwelling for the past 10 million years, with upwelling cells shifting in position and intensity through successive ten- and hundred-thousand year fluctuations in sea level (e.g., Shannon, 1985; Diester-Haass et al., 1992). The northern boundary of the system is the warm, saline Angola current, while to the south, at ~34° S, the warm Agulhas current predominates (Shannon, 1985; Shannon and Nelson, 1996; Hutchings et al., 2009).

The Benguela upwelling system can be divided to a northern and southern section just north of Lüderitz, where a pronounced (partial) divergence of the current occurs (Shannon, 1985; Shannon and Nelson, 1996; Hutchings et al., 2009). The northern Benguela coastline is bounded to the east by the arid Namib Desert, with the Kunene River to the north as its only constant supply of fresh water (e.g. Boyer et al., 2000). The width of upwelling ranges on average from 150 to 200 km from the coast and its intensity increases along narrow parts of the shelf and decreases along wider parts (Longhurst, 1998; Boyer et al., 2000 and references within). The northern Benguela upwelling system is characterized by persistent, though less intense, upwelling as compared to the southern Benguela (e.g. Longhurst, 1998). Productivity is

greatest in the north (Bremner, 1983), with typically lower seafloor oxygen levels (Bailey, 1991; Shannon and Nelson, 1996; as low as <<0.5 ml/l; Hutchings et al., 2009).

3. Materials and methods

Box- and gravity-core samples of the Walvis shelf were taken in 1972–74 by G.F. Birch, J. Rogers and J.M. Bremner (Birch, 1975), while on the R/V THOMAS B. DAVIE during the strongest upwelling season between mid-December and mid-March. Their sampling grid of 10 nautical miles extended from the shore at ~20–2000 m water depth. The area investigated in the present study focused on existing samples from the northern half of the Benguela upwelling system (25°S–17°S, corresponding to Michael Bremner's Ph.D. field area, 1978), which holds the highest concentrations of organic matter within the system, as well as some of the lowest bottom-oxygen concentrations (0.06 ml/l at 17°S, Zettler et al., 2009). The northern Benguela upwelling system is not influenced by the large terrigenous input of the Orange River to the south. On average the samples are thought to represent only the past ~5000 or less years (Bremner, 1983).

Existing grab samples from the northern area were examined in two ways for ecologic analysis of molluscan death assemblages. (1) A random subset of samples (total 16) was taken from each end-member sediment type present on the shelf. Sediment type was based on lithologic information from the lithofacies maps of Bremner (1978) and Rogers and Bremner (1991). The end-member samples were taken from sediments containing maximum weight-percentages of opal, organic matter, CaCO₃ and phosphate that were 50–88%, 19–24%, >75% and >20%, respectively (Fig. 1). (2) Ten samples were examined from an onshore-offshore transect located at approximately 25°S. This transect extended from shallow-offshore (38 m) to slope depths (1500 m) and was positioned to intersect with as many sediment types as possible. The physical description for all twenty six samples is given in Table 1.

Individual samples were weighed, sub-sampled to approximately 100 grams dry weight, and gently wet sieved through both a >1 mm and >2 mm sieve. The fractions were oven dried at 50 °C. The >2 mm fraction was picked and counted for shelly macrofaunal remains. The >1 <2 mm fraction was further surveyed for species not found in the coarser fraction; however, no additional species were encountered in this size fraction. This procedure was repeated for additional 100 gram sub-samples until no new species were added and at least 100 specimens were counted. In samples of low volume or low shell abundance, the entire sample was sieved and counted to maximize the number of counted individuals. Samples were also scanned for the presence of benthic foraminifera (macrofaunal count-data for the samples are given in Supplementary Data 1). The taxa were identified to the lowest taxonomic level possible, using published taxonomic monographs (e.g., Brown and Jarman, 1978; Kilburn and Rippey, 1982; Steyn and Lussi, 1998) and with the help of a sample reference collection assembled by John Pether, an independent molluscan expert. Valentine et al. (2002) was used to determine gastropod feeding modes.

In order to find associations between samples and ecological variables, the data were organized into a matrix based on percent abundance of each species. A cluster analyses (using Euclidean distance to construct a dissimilarity matrix) was employed to find associations between the samples. The “R” Free Software package (<http://www.r-project.org/>) was used to conduct the multivariate analysis using M. Foote's Q-mode clustering analysis program.

Variation in benthic community structure was examined using **species richness** (number of species per sample) and **species evenness** (how uniformly individuals are distributed among the different species). Both indices usually decrease with increasing environmental stress (e.g., Rhoads and Morse, 1971; Rosenberg, 1976; Clarke and Warwick, 1994; Levin et al., 2002). Species richness in particular is sample-size dependent. Thus, in order to compare between samples in

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