

Chemosymbiont-dominated seafloor communities in modern and Cretaceous upwelling systems support a new, high-productivity variant of standard low-oxygen models

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ABSTRACT

Faunal analysis of modern (Benguela upwelling system, Namibia) and ancient (upper Cretaceous, Israel) sedimentary records rich in organic matter, biogenic silica, carbonate, and phosphate indicates that, contrary to stereotypes of upwelling systems as dead zones, macrobenthic communities are present but highly variable. Biofacies vary with distance from the upwelling core and as a function of both the supply of food to the seafloor and the oxygen demand it creates there: under a high organic supply, large-bodied chemosymbiotic bivalves dominate exaerobic and lower dysaerobic seafloors, and deposit feeders are abundant in upper dysaerobic and aerobic zones. Macrobenthic biofacies under upwelling thus contrast strongly with the overwhelmingly filter feeder-dominated biofacies encountered in the dark siliciclastic shales on which standard oxygen-restricted biofacies models have been based, and argue that, mechanistically, the low-oxygen conditions characterizing those shales reflect ordinary levels of water-column productivity and arise largely from water-column stratification. Our biofacies model requires testing in other upwelling records. However, we expect it to be robust and useful given the long evolutionary histories of the chemosymbiotic and deposit-feeding guilds, providing a new means for discriminating the relative roles of high organic flux and low ventilation in creating low-oxygen conditions at the seafloor.

INTRODUCTION

Factors governing the deposition of silica-, organic carbon-, and phosphate-rich sediments in highly productive upwelling systems are complex, such that many fundamental questions about the variability and drivers of bottom-water oxygen levels remain unclear (Parrish, 1998; Levin, 2003). This situation has been exacerbated by the diagenetic lability of such sediments (Soudry et al., 2006; Hatcher et al., 2014), which complicates geochemical inference. In other natural settings, paleo-oxygen gradients are reconstructed from trace-fossil and body-fossil evidence with considerable confidence, building on the work of Rhoads and Morse (1971): with decreasing oxygen, seafloors are characterized by a less diverse, less calcified, smaller bodied, and more exclusively epifaunal macrobenthic fauna and by lower bioturbation indices (e.g., Savrda et al., 1984; Savrda and Bottjer, 1991). Ecological and paleoecological studies show that the taxonomic composition of shelly macrobenthos can be diagnostic and that oxygen levels are temporally variable (Rhoads et al., 1991; Wignall, 1994; Boyer and Droser, 2007, 2009; Gooday et al., 2009).

The seafloors of upwelling systems also typically exhibit oxygen gradients, with anoxia developing in core areas where cells of upwelling nutrient-rich water are most persistent on an annual to interannual basis and organic matter flux to the seafloor is highest. We can thus expect that macrobenthic abundance, richness, community structure, and body size will vary along

oxygen gradients in upwelling systems, but possibly in different ways than under the lower levels of primary productivity that characterize most shelves and inland seas. Understanding biofacies variation in high-productivity settings is important for stratigraphic analysis in order to discriminate (1) oxygen depletion associated with upwelling and other oceanic eutrophication from (2) depletion that arises largely from water-column stratification alone (e.g., oxygen minimum zones and oceanic anoxic events; Rabalais et al., 2010).

Here we present the first quantitative evaluation of shelled macrobenthic invertebrate assemblages under upwelling conditions, using both modern and ancient settings, and propose a new dedicated low-oxygen model. We stress diversity and functional groups rather than taxonomy in order to identify patterns that are robust across geologic time.

METHODS

The modern Benguela upwelling system (BUS) offshore of Namibia is one of the major eastern boundary upwelling systems (Shannon et al., 2006; Hutchings et al., 2009) (Fig. 1). Sediments on this broad continental shelf contain the highest organic matter contents known in any modern upwelling areas (as high as 25 wt%), with siliceous and carbonate oozes and patches rich in authigenic phosphorite (>20 wt%; Bremner, 1978; Rogers and Bremner, 1991; Compton et al., 2004). Highest productivity and lowest bottom-water dissolved oxygen levels occur

close to shore (Bailey, 1991). These conditions contrast with other perennial systems such as Peru, where upwelling is most intense over deep seafloors (~700 m) due to the steepness of the shelf, and northwest Africa, where water energy prevents anoxic conditions and ooze accumulation on the shelf (Filipsson et al., 2011). The upper Cretaceous (Campanian) Mishash Formation (MIS) of Israel provides an ancient counterpart from the southern coast of the Tethys, another passive margin setting. The MIS comprises an ~9 m.y. record of organic-rich carbonate, porcelanite, chert, and phosphorite from one of the most extensive high-productivity complexes known in the stratigraphic record (Soudry et al., 2006; Edelman-Furstenberg, 2009).

Molluscan data for the modern BUS were sieved from 17 box cores of organic-rich diatomaceous (opal) and biogenic carbonate (micrite) oozes and phosphate-rich shell gravels collected

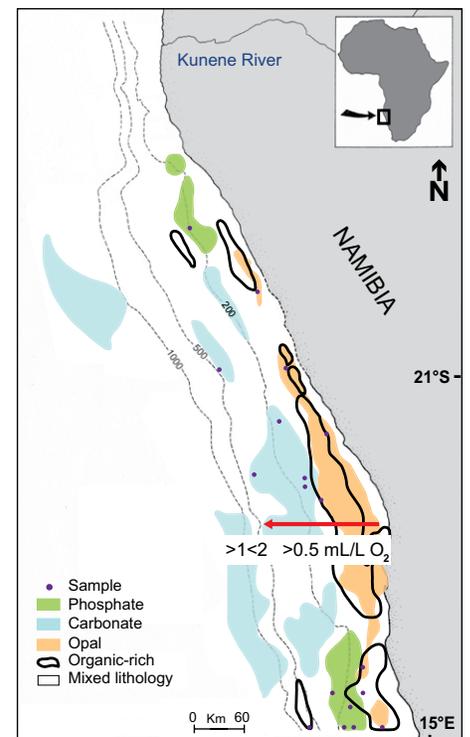


Figure 1. Facies map of the modern Benguela upwelling system (adapted from Edelman-Furstenberg, 2014, building on Bremner, 1978). Oxygen increases offshore (red arrow) toward shelf break.

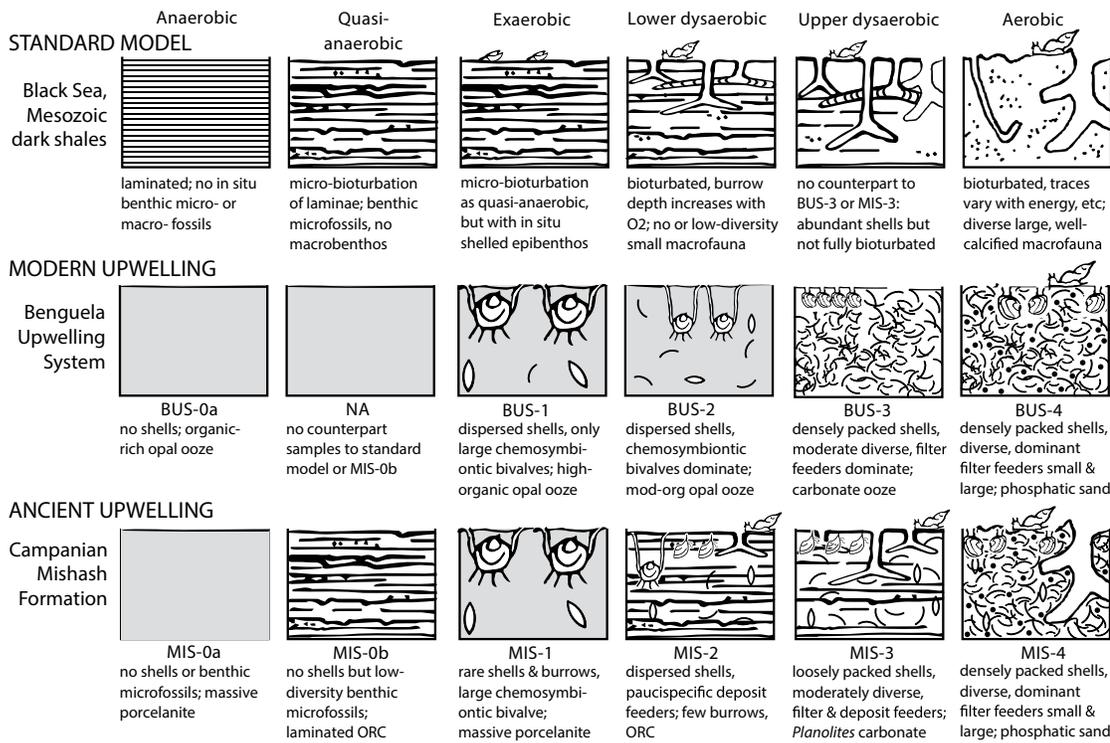


Figure 2. Comparison of the standard low-oxygen biofacies model (Rhoads and Morse, 1971; Savrda et al., 1984; Savrda and Bottjer, 1987; Rhoads et al., 1991; Wignall, 1994) (top row) with upwelling-variant biofacies recognized here. ORC—organic-rich carbonate; mod-org—moderately organic.

on the Walvis shelf in 1972–1974 by G.F. Birch, J. Rogers, and J.M. Bremner (Bremner, 1978) (Fig. 1). Bivalve specimens of >2 mm preserving at least half of the hingeline and gastropod specimens with an intact apex were counted as individuals (Table DR1A in the GSA Data Repository¹). Comparable field counts were collected from bedding planes and rock fragments from each of the four main lithologies within the Phosphate Member of the Mishash Formation, namely massive porcelanite, organic-rich carbonate, thin-bedded porcelanites, and phosphate-bearing shell beds (22 samples total; Table DR1B).

RESULTS

In each study area, faunal samples clustered into four biofacies based on differences in the proportional abundance of mollusk species (Edelman-Furstenberg, 2008, 2009, 2014), plus a fifth (0) biofacies introduced here to accommodate samples that lack mollusks (Fig. 2; Fig. DR1). Biofacies are numbered analogously, using the prefixes BUS and MIS, and occur in similar sediment types. Qualitatively: biofacies 0 lacks mollusks, occurs in very high-organic silica (massive porcelanite) and, in the MIS only, is in laminated organic-rich carbonate; biofacies 1 comprises only chemosymbiotic bivalves, and

occurs in very high-organic silica; biofacies 2 is paucispecific, dominated by chemosymbiotic or deposit-feeding bivalves, and occurs in high-organic silica (BUS) and organic-rich carbonate (MIS); biofacies 3 is moderately diverse, and occurs in carbonate; and biofacies 4 is diverse, and occurs in phosphate-rich shell gravels with scant mud. Both study areas also show similar increases in bioturbation index, shell packing density, and shell damage (Table DR1). In BUS, biofacies and lithotypes are arrayed along a gradient of measured bottom-water oxygen from <0.5 mL/L to >2 mL/L (Bailey, 1991; Fig. 1; Table DR1A). In the MIS, each lithotype displays a different intensity and type of ichnofabric (Table DR1B) similar to those that Savrda and Bottjer (1991) associated with benthic oxygen levels from <0.01 to >1 mL/L.

Diversity trends are similar in the two study areas: sample size-adjusted species richness (Margalef's diversity index D) differs significantly among biofacies (analysis of variance, ANOVA, $p < 0.05$), and both richness and evenness (sample size-insensitive Hurlbert's probability of an interspecific encounter, PIE) increase from biofacies 1 to 4 (Fig. 3A). The MIS biofacies richness does not, on average, differ significantly from its modern BUS counterpart, and evenness values in the two areas match well in biofacies 1 and 4.

Both study areas also exhibit similar trends in trophic groups: biofacies 1–4 decrease in the proportional abundance of bivalves that rely on dead organic matter, i.e., deposit-feeding nuculanids and chemosymbiotic lucinids, which benefit from sulfate-reducing microbes and are

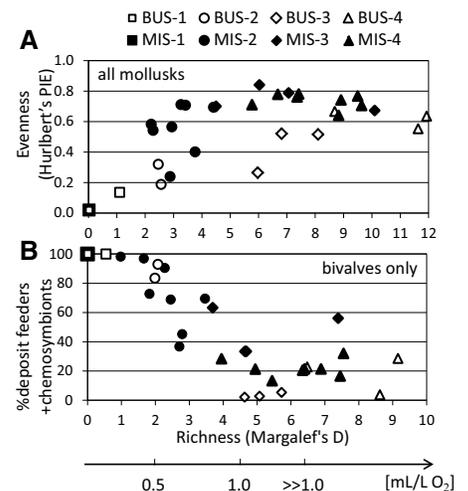


Figure 3. A: Variation in evenness and species richness among modern Benguela upwelling system (BUS) and ancient Mishash Formation (MIS) molluscan biofacies. Both diversity measures increase with increasing bottom-water oxygen levels, based on oxygen data from BUS (Bailey, 1991). A richness (Margalef's diversity index D) of zero and evenness (Hurlbert's probability of an interspecific encounter, PIE) of zero denote a monospecific assemblage. B: The combined percent abundance of chemosymbiotic and deposit-feeding bivalves, scaled against the richness of bivalves only, decreases with increasing oxygen levels and decreasing organic matter, reflecting distance from the core of the upwelling system.

¹GSA Data Repository item 2015329, Figure 1 DR1 (cluster analysis) and Table DR1 (biofacies composition and environmental information), is available online at www.geosociety.org/pubs/ft2015.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

tolerant of dysoxic waters (Taylor and Glover, 2000, 2010; Fig. 3B; Table DR1). These bivalves dominate biofacies 1 and 2 in both fossil and modern areas, but are scarce in biofacies 3 and 4, where filter-feeding bivalves dominate.

In both study areas, and contrary to expectations of smaller body sizes with increasing stress, the average body size of chemosymbiotic lucinids is higher in biofacies 1 (to 45 mm in length) than in oxygenated biofacies 3 (as large as 16 mm in BUS or 25 mm in MIS) (Table DR1). Other species occur in fewer biofacies and do not vary significantly in body size.

COMPARISON WITH STANDARD LOW-OXYGEN MODEL

Macrobenthic assemblages from both upwelling records can be categorized readily using the oxygen-related models developed by others using body fossils and trace fossils from settings of average or low productivity (Fig. 2, top). For example, in our upwelling records, sample size-adjusted diversity increases, by an order of magnitude, from monospecific assemblages in the exaerobic and lower dysaerobic biofacies to the (shell rich) upper dysaerobic and aerobic facies (Fig. 3A), as also observed along paleo-oxygen gradients in dark shales (e.g., Savrda and Bottjer, 1991; Wignall, 1994; Boyer and Droser, 2007, 2009). The bioturbation index similarly increases from biofacies 1 (intact laminations) to 4 (large, deeply penetrating burrows; Table DR1).

However, biofacies in upwelling systems differ significantly from standard dark shale models in several key ways: (1) the importance of infaunal bivalves of unquestioned chemosymbiotic lifestyles in the exaerobic and lower dysaerobic zones, rather than opportunistic epibenthic filter feeders; (2) the large rather than exclusively small body sizes there, owing to successful chemosymbiotic species; (3) the relatively large role of deposit feeders, which can equal or exceed the importance of filter feeders; and (4) the very high shell content of the seabed in the upper dysaerobic to aerobic margins of the upwelling core, which probably reflects dense molluscan populations rather than time-averaging alone. These differences signal the role of food availability in addition to bottom-water oxygenation, both functions of distance from the core of the upwelling system, in controlling macrofaunal distribution.

Chemosymbiotic bivalves characterize settings of high and relatively steady organic supply such as cold seeps, seagrass beds, and wastewater-affected seafloors where H_2S -rich sediments exist within burrowing depth (Taylor and Glover, 2000, 2010). All lucinids exhibit this symbiosis, which is likely obligate (Taylor and Glover, 2010). The importance of large-bodied lucinids in our upwelling records shows that organic flux was exceptionally high and low-oxygen bottom waters arise from the high

biological oxygen demand created by this flux rather than from poor ventilation alone. Previous workers postulated that chemosymbiotic bivalves should be present in exaerobic and lower dysaerobic black shales, but they are apparently absent (Wignall, 1994; Knight et al., 2014). Rare specimens have been reported from the Miocene Monterey Formation (an unusual anadardid; Savrda and Bottjer, 1987) and modern California slope (Bottjer et al., 1995); both settings have seasonal upwelling.

Our monospecific assemblage of chemosymbionts contrasts strongly with those of filter-feeding epifauna that opportunistically colonize low-oxygen seafloors in nonupwelling systems (e.g., Wignall, 1994; Boyer and Droser, 2007, 2009). Deposit feeders are also more important in low-oxygen seafloors in upwelling, rather than nonupwelling, systems (our lower and upper dysaerobic biofacies 2 and 3). Deposit feeders are rare in shelly assemblages in Devonian black shales (Boyer and Droser, 2009) and are not mentioned from Mesozoic black shales (Wignall, 1994). Neither chemosymbiotic nor deposit-feeding bivalves are listed in a Phanerozoic review of common dysaerobic groups (Allison et al., 1995), even though modern-day organic-loving families range in the geologic record back to the early Paleozoic.

We thus propose a parallel set of low-oxygen biofacies for upwelling systems, characterized in functional rather than taxonomic terms, that can be used to distinguish low-oxygen macrobenthic assemblages produced under conditions of high productivity (Fig. 2).

Upwelling Biofacies 0a (Anaerobic)

In the standard model, bottom water is continuously anoxic, disallowing even benthic microfossils. The upwelling biofacies is comparable but the seafloor is biogenic silica.

Upwelling Biofacies 0b (Quasi-Anaerobic)

In the standard model, episodes of partial aeration permit colonization by unicellular eukaryotes. The upwelling biofacies is comparable but the seafloor is (laminated) organic-rich carbonate ooze.

Upwelling Biofacies 1 (Exaerobic)

In the standard model, low-oxygen bottom water disallows active metazoan bioturbators but permits successful colonization and maturation of a rare, sessile, shelled epibenthos. In upwelling systems with similar oxygen, the high supply of organic matter supports abundant infaunal chemosymbiotic lucinids, which grow to large body size.

Upwelling Biofacies 2 (Lower Dysaerobic)

In the standard model, fluctuating but mostly dysoxic bottom water permits colonization and maturation of a moderately diverse molluscan

fauna, but with limited penetration of the seafloor by bioturbators. The upwelling fauna is also moderately diverse, but organic matter flux is sufficient for chemosymbionts (BUS-2) or deposit feeders (MIS-2) to dominate, and the seafloor is either biogenic silica or organic-rich carbonate.

Upwelling Biofacies 3 (Upper Dysaerobic or Transitional)

In the standard model, fluctuating but mostly aerobic or nearly aerobic bottom water permits colonization and maturation of more diverse mollusks and deeper penetrating bioturbators. Marginal to the core upwelling area, shallow-burrowing filter feeders (BUS-3) or a mix of filter- and deposit-feeders dominate (MIS-3). Relatively well preserved and abundant shells in the carbonate-mud matrix suggest large mollusk populations rather than time-averaging alone, perhaps analogous to the aggregations of macrofauna observed along the edges of modern oxygen minimum zones (Levin, 2003; Gooday et al., 2009).

Upwelling Biofacies 4 (Aerobic)

In the standard model, continuously aerobic bottom waters support high molluscan diversity and a well-mixed, *Thalassinoides*-burrowed seabed. Counterpart upwelling seafloors are phosphorite-rich shell gravel, with scant mud and a mix of trophic groups and a relatively high proportion of attached epifauna, suggesting a dynamic mosaic of shelly to muddy conditions. Exclusively disarticulated bivalve shells and mixed levels of shell damage suggest more time averaging than in biofacies 3, but populations were probably still large. Heterozoan shell gravels of the northwest African shelf (Klicpera et al., 2015) are probably analogous, albeit from the margin of a less intense upwelling system (Filipsson et al., 2011).

CONCLUSIONS AND IMPLICATIONS

Modern and ancient upwelling records are remarkably similar at multiple levels of biological organization, i.e., richness, evenness, dominant trophic groups, and body size, demonstrating the robustness of faunal patterns across upwelling systems, notwithstanding the intervening Late Cretaceous extinction. However, these biofacies differ significantly from standard oxygen-restricted biofacies models developed by others for dark shale records, probably due to the high and steady flux of food to the seafloor. That flux permits the development of a distinctive, stable, low-diversity community of chemosymbiotic bivalves under the upwelling core, where high biological oxygen demand magnifies low-oxygen conditions in bottom waters. With increasing distance from the upwelling core, food supply continues to be higher than in normal-productivity settings,

supporting communities rich in deposit feeders and, at the aerobic margin, especially large populations of filter feeders. The low-oxygen macrobenthic communities encountered in the distinctive biogenic sediments under upwelling thus contrast strongly with the overwhelmingly filter feeder-dominated communities encountered in siliciclastic dark shales. This situation suggests that, mechanistically, the low-oxygen conditions characterizing those shales reflect ordinary levels of water-column productivity and arise largely from water-column stratification.

Our upwelling biofacies model requires testing in other modern and ancient settings. However, we expect it to be robust given the long evolutionary histories of the chemosymbiotic and deposit-feeding guilds among bivalves. Distinguishing the relative importance of high organic flux and low ventilation is geologically important given the widespread distribution of dark shales, marls, and carbonates at key intervals in geologic history (ocean anoxic events) and the importance of recognizing upwelling zones for paleogeographic and paleo-oceanographic reconstruction. It is also important given the increasing number of dead zones in modern coastal seas: some are attributed to the runoff of cultural nutrients from land (elevated surface-water productivity) and others to secular warming, which reduces mixing and permits the shoreward expansion of oxygen minimum zones (reduced ventilation; Rabalais et al., 2010). Paleocological analysis of shelly macrobenthic assemblages, particularly analysis stressing functional rather than taxonomic groups, should provide a sensitive means of ranking key variables in the formation of low-oxygen seafloors.

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