



Preface

“Coastal hypoxia and anoxia: a multi-tiered holistic approach”

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Hypoxia and anoxia have played pivotal roles in shaping animal communities in both ancient and modern continental shelf seas. The range extends from millennia-long, global phases such as oceanic anoxic events (OAE) (Jenkyns, 2010) in earth’s history to the days- to months-long coastal oxygen crises of the Anthropocene (Crutzen, 2002). Nonetheless, for benthic communities – whether past or present – the challenges and the responses to low dissolved oxygen concentrations are no doubt similar. This led early on to attempts to establish bridges between workers in the fields of geology/sediment geochemistry, paleontology, marine ecology and physiology, including synchronizing the anoxia-related terminologies depending on whether the terms are applied to environments, biofacies or physiological responses of living organisms (e.g., Tyson and Pearson, 1991).

Since those earlier attempts, hypoxia and anoxia have become ever more pressing issues. Among the many threats facing shallow coastal waters, such as pollution with oil, heavy metals or halogenated hydrocarbons, only one, namely eutrophication and its ultimate symptom – oxygen depletion – is capable of severely modifying and extinguishing most macrofauna over large areas. Anoxia can last briefly or as long as millennia, triggering “local” mortalities to mass extinctions. The number of affected areas has increased rapidly, with currently almost 500 so-called dead zones being recognized worldwide (Diaz et al., 2010). The largest areas today extend over several thousand square kilometers (e.g., Gulf of Mexico) and there is convincing evidence that human activities beyond eutrophication, e.g., climate change, will exacerbate the frequency, duration and intensity of both natural and human-induced hypoxia in the near future (Gruber, 2011). The expansion of oxygen minimum zones (OMZs), with its implications for both the pelagic and benthic realms, is a further cause for concern (Levin, 2003).

Eutrophication and dead zones require rethinking the term “extreme environments”. Traditionally, extreme referred to very high/low temperatures, high/low salinities, great depths, etc. – individual parameters at the far end of the natural range. Nonetheless, such conditions are often consistent enough to enable adaptation by communities. The concept of extreme environments has rarely been applied to shallow shelf seas. Whether anoxia is seasonal, periodic, or episodic, however, its alternating “off-on”, “all-or-nothing” property makes affected areas more inhospitable than classical “extreme” habitats: little adaptation is possible and a minimalistic set of “lowest-common-denominator” species tend to dominate (Pearson and Rosenberg, 1978). Our work therefore addresses the issue of environments that are extreme but consistent versus those that are extreme because of wide fluctuations.

Commensurate with the insidiousness of the threat (“rapid death, slow recovery”; Stachowitsch, 1991), many studies have been conducted in particular seas or on selected species/communities, and first meta-analyses (e.g., Vaquer-Sunyer and Duarte, 2008) have pieced together the results to provide a better overview (Zhang and Gilbert, 2010). The current effort was designed to concurrently examine a wide level of resolution, organization and duration at one site, from sediment geochemistry to meiofauna to macrofauna ecology. The approach is based on experimentally inducing hypoxia/anoxia using benthic chambers positioned on the sediment surface at 24 m depth in Slovenian waters of the Gulf of Trieste, Northern Adriatic Sea, Mediterranean. The deployments ranged from days to months to almost 1 year (~ 10 months). Over the short term, a time-lapse camera was used to document the macrofauna (in- and epifauna) behavior and mortality during decreasing oxygen concentrations. In the longer-term experiments (1 month, 2 months, 10 months), sediment cores for meiofauna and sediment geochemical

analyses were taken and gel probes (DETs, diffusive equilibration in thin films) deployed. Macroepifauna scavenging and recovery in two experimental plots was documented with a camera (from days up to 2 years).

In coastal environments such as the Northern Adriatic Sea, oxygen penetration within the sediment is often only a few millimeters. While some infaunal species do inhabit the anoxic part of the sediment (e.g., meiofauna, Bernhard et al., 2003), infaunal microhabitats are typically vertically limited by the presence of toxic sulfide. Anoxia-related upward shifts of redox zones release reduced components such as Mn(II), Fe (II) and S(-II) to the water column, further poisoning benthic communities. The hypothesis is that the infauna and the epifauna react accordingly with shifts, altered compositions and mortalities. The present special issue examines the changes in the sediment and at the sediment–water interface, the accompanying responses of the benthic meio- and macrofauna, and the post-anoxia processes. This interdisciplinary effort complements the often serendipitous observations of low-oxygen events in the field and yielded an insightful mosaic enabling a broader synthesis.

Metzger et al., 2014 describe the evolution in the vertical distribution of several redox-sensitive species at a millimeter scale using gel probes (DETs). Beyond the upward shifts of manganese, iron and sulfate reduction zones, unexpected features such as downward flux of sulfides due to macrofauna decomposition were recorded as well. Thus, benthic mortalities affected the geochemistry by producing sulfide at the sediment–water interface, generating diffusion of sulfide from the overlying water to the sediment. This, in turn, controlled upward diffusion of reduced iron. The lack of this phenomenon later in the experiment (i.e., no free sulfide in the system) was interpreted to reflect exhaustion of fresh organic carbon at the sediment surface. Within the sediment, despite evidence of sulfate reduction, almost no free sulfide was recorded; this suggested a strong control of sulfide mobility by solid iron oxide phases. These processes were useful in explaining changes in the infaunal microhabitats and the reactions of the benthos.

Grego et al., 2014 assess the impact of the above geochemical processes on the mortality rates of selected metazoan meiofauna groups (copepods, nematodes) during hypoxia and anoxia. This involved comparing two techniques to enumerate meiofauna: labeling with CellTracker Green (CTG), a vital fluorogenic probe developed to stain only living cells/animals, and staining with the more traditional, non-vital biological stain Rose Bengal (RB). The latter significantly overestimated the number of living copepods because it also marked freshly dead but not yet decomposed individuals. The CTG approach better resolved the initial, fine-scaled processes. This approach, already accepted for Foraminifera (Bernhard et al., 2006), is therefore also valid for other meiofauna groups.

De Troch et al., 2013 determine that anoxia in a short-term (5 days) in situ experiment significantly impacted copepod abundance but not family diversity. Ectinosomatidae and Cletodidae were most abundant in both normoxic and anoxic samples. Harpacticoid copepod family diversity was significantly affected only by sediment depth. Nematode densities were unaffected by anoxia or sediment depth. Additionally, a laboratory tracer experiment with ^{13}C -prelabeled diatoms as a food source for copepods was conducted to test whether the supply of additional food could improve their survival in anoxia. The provision of diatoms did not affect the survival rate; that rate was affected only by oxygen levels and was higher in normoxia than in anoxia. Anoxia, however, considerably reduced the grazing pressure on diatoms as copepods stopped feeding. Accordingly, anoxia affected the survival of both the consumers (direct effect) but also of primary producers (indirect effect), which has important implications for the recovery phase.

In a second contribution, Grego et al., 2014 examine the longer-term impact of anoxia on the copepod community. Supporting and expanding upon the findings of De Troch et al., 2013 above, the copepod family Cletodidae (various species from the genera *Cletodes*, *Stylicletodes*, *Enhydrosoma* and *Acrenhydrosoma*) survived 1 and a few specimens even 2 months of anoxia. This surprising survival in extended anoxia is interpreted to reflect their specific feeding ecology and rapid reproduction as soon as the oxygen level rises. Nonetheless, there was little short-term immigration into the experimental plots from the surrounding sediment. The allocation of energy to reproduction (significant increase in number of gravid females) immediately after the stress event was remarkable. Beyond being highly resistant to anoxia, all species of this family are also very resilient. This underlines the strength of species-based response analyses.

Langlet et al., 2014 determine that foraminiferal faunas (> 63 μm test size and CTG stained) were alive at every phase of oxygen decline, even after 10 months of anoxia. Living individuals were found alive – supported also by Ribosomal RNA analysis – at every sediment depth (from 0 to 5 cm). The total foraminiferal density decreased exponentially with the duration of anoxia, but the decrease took place mostly at the sediment–water interface (0–0.5 cm depth). Interestingly, foraminiferal density increased after 1 month of anoxia. The authors hypothesize that this increase is a response to increased organic matter availability due to the degradation of dead macrofauna, an interpretation supported by the geochemical data. The conclusion is that the Adriatic Sea foraminiferal faunas are highly resistant to anoxic conditions. Their density variations over time appear to be less a direct response to anoxia than to fluctuations of labile organic matter availability.

In a companion paper, Langlet et al., 2014 more closely examine the effect of the experimentally induced anoxia on the foraminiferal assemblages. Although no major changes in species composition or biodiversity were observed, both

density and species richness decreased during the experiment (9 days to 10 months). The individual responses of the major species are characterized. *Reophax nanus*, *Textularia agglutinans* and *Quinqueloculina stelligera* were sensitive to anoxia and showed a strong density decrease with time. Most other taxa, including *Eggerella scabra*, *Bulimina marginata*, *Lagenammia atlantica*, *Hopkinsina pacifica* and *Bolivina pseudoplicata*, exhibited no strong density changes over time and were apparently highly resistant to anoxia. The increased standing stock of the anoxia-sensitive *Quinqueloculina seminula* after 1 month was attributed to decomposing macrofauna and the resulting pulse of organic matter. The survival of most species under the induced anoxic conditions probably reflects an adaptation to the frequently occurring periods of severe oxygen depletion in the Northern Adriatic Sea. A further explanation for survival – the possibility of anaerobic metabolism – was tested for some species. Measuring the intracellular nitrate cell content and denitrification rates under laboratory conditions revealed that none accumulated nitrates: in these species, tolerance to long-term anoxia is apparently not due to a capacity to denitrify.

In a parallel effort involving a different area and a different approach, Ishimura et al., 2012 examine the stable carbon and oxygen isotopes in tests of individual, Rose Bengal-stained benthic foraminifera from the continental margin of the northwestern Pacific Ocean. Based on the inter-individual isotopic variations, the authors were able to select suitable species as bottom-water proxies. This represents a step forward in using isotope data of benthic foraminifera to help reconstruct past bottom-water conditions and evaluating global carbon cycling.

The first easily visible signs of hypoxia and anoxia are changes in macrofauna behavior. Riedel et al., 2014 use the visibility and location of the in- and epifauna, as well as their locomotion, body movement, body posture, interactions and other species-specific features to detail the varied behavioral responses of the benthic fauna. Most of these behaviors – documented in 10 000 time-lapse camera images – were correlated to specific oxygen thresholds. Sensitive (i.e., brittle stars) and more tolerant (i.e., gastropods) species are distinguished, various survival strategies outlined, and a catalog of reproducible and predictive behaviors for all common species presented. A synthesis attempts to outline the broad response categories and indicates the overall impact of progressively decreasing oxygen concentrations on broader ecological processes. In an age of increasingly simplified video opportunities, such stress reactions can increasingly be documented by marine biologists, technicians, divers and fishers, helping transport such complex processes to the public and decision-makers.

Often-posed questions are what happens after an oxygen depletion event and how long does macrofauna recovery take? The Blasnig et al., 2013 contribution tackles these issues by using time-lapse camera sequences to determine that scavengers arrive in a distinct sequence related to the den-

sity, relative speeds and anoxia tolerance (survival) of the organisms: fishes arrived first, followed by hermit crabs and gastropods shortly after anoxia. The organic remains of the dead organisms are consumed within 1–2 weeks, leaving a denuded bottom. Images taken 1 and 2 years after the anoxia revealed no macroepifauna recovery in the two experimental plots. The validity of extrapolating the small-scale experiments to large-scale collapses, along with the role of larval settlement and immigration, is discussed. This supports the interpretation that recolonization of this soft-bottom habitat is a long-term process requiring certain prerequisites, for example biogenic structures on which the sessile epifauna can settle.

1 Synthesis

Hypoxia- and anoxia-induced changes occur at all levels of the benthos. The sediment biogeochemistry underwent major – and very differentiated – shifts in the studied metal, nutrient and organic matter concentrations during the successive normoxic to anoxic to re-oxygenated phases. These changes clearly affected the meiofauna. As expected, the copepods were more sensitive than the foraminiferans but, again, the responses within the individual groups were highly differentiated: some copepod families were unexpectedly tolerant, and many foraminiferan taxa survived nearly 1 year of anoxia. The results show that this survival was not linked to known alternate energy pathways (i.e. no anaerobic metabolism involving denitrification for the tested species). The macrobenthos responded to declining oxygen concentrations with a series of predictable behavioral responses, ultimately ending in the mortality of most species within days and attracting a predictable sequence of scavengers.

The feedback loops of direct and indirect effects that became evident through the in situ experimental approach linked all ecosystem levels and significantly defined the overall benthic responses. Not only did declining dissolved oxygen directly alter sediment biogeochemistry and faunal composition, but the decomposition of the benthos, in turn, significantly affected sediment geochemistry: the presence and distribution of sulfides were determined in part by decaying organic material, which apparently even increased the density of certain foraminiferans after 1 month of anoxia. Rather than an upwardly migrating redox layer governing the many processes and subsequent mortalities, the processes at the sediment–water interface affected the sedimentological processes. This sheds new light on the potential role of another source or organic matter, namely the massive settling marine snow that often accompanies oxygen crises in the Adriatic Sea. Finally, during the recovery phase, the differentiated and often variable sedimentological features are in part attributed to bioturbation by surviving infauna species and recolonizers.

The scientific impact of a study at a particular site is multiplied if the results are more generally valid and transferable. We believe this to be the case, as exemplified by the similar responses of the macroinfauna and -epifauna in other coastal soft-bottom communities. Thus, the similarity of taxa and functional groups that gave rise to the parallel- or iso-community concept might be reconsidered in light of similar responses and other commonalities in the response to hypoxia/anoxia worldwide. Knowledge on the sequences of behaviors and mortalities can yield information on the current status of a benthic community and even serve an early-warning function. The recognition of tolerant species, combined with knowledge about recovery processes and their speeds (including growth rates of opportunistic species and other recolonizers) can help evaluate longer-term status, for example help narrow down the time of past mortalities and assess the effect of repeated disturbances.

The complex effects of and responses to hypoxia/anoxia encompass the full range of ecosystem-relevant issues including stability, disturbance, ecosystem shifts, recovery, biodiversity, and shifting baselines. What do we know and what can we do? We know a lot, or at least enough to apply common sense and take action to reduce nutrient inputs into the sea and minimize the synergistic effects of multiple stressors. This calls for activating the full range of policy and management tools to promote remediation and optimize ocean governance. What can we hope for? That our targets are not too modest, not diluted with a priori compromises, and that further community depauperations and impaired ecosystem services will not cause irreparable harm.

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