

Dead zones: a future worst-case scenario for Northern Adriatic biodiversity

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Abstract

Shallow coastal seas are most endangered (Halpern et al., 2008) and, through a series of impacts ranging from overfishing, eutrophication to coastal development, they are likely to experience the largest change in biodiversity should present trends in human activity continue (Jenkins, 2003). No other crucial environmental variable has changed more drastically in shallow coastal marine ecosystems worldwide than dissolved oxygen (DO) (Diaz, 2001). “Dead zones”, caused by hypoxia ($DO < 2.0 \text{ ml l}^{-1}$) and anoxia (no oxygen) in bottom-water layers, top the list of emerging environmental challenges (UNEP, 2004), and the problem is likely to become worse in the coming years (Wu, 2002; Selman et al., 2008).

The Adriatic Sea is the most impacted system of the entire Mediterranean (Danovaro, 2003; Lotze et al., 2006). Over the last decades, increasing nutrient and organic loads have triggered considerable environmental changes, with an enhanced frequency and severity of benthic dystrophic events (Danovaro and Pusceddu, 2007).

We provide here a brief overview of low DO events in the Northern Adriatic and responses from the species to the ecosystem level. The potential coupling between climate factors and coastal eutrophication is discussed.

Northern Adriatic hypoxia

The Northern Adriatic Sea is a recognized area for long-term decreases in DO concentration and associated benthic community changes and mortalities (Stachowitsch, 1984, 1991; Justić et al., 1987). It combines many features known to be associated with low DO events (Stachowitsch and Avcin, 1988): it is semi-enclosed, shallow (<50 m) and is characterized by soft bottoms, a high riverine input (mainly from the Po River), high productivity and long water residence times (Ott, 1992). As elsewhere in the northern hemisphere, this constellation can be associated with seasonal hypoxia and anoxia in late summer/early fall. Moreover, the combination of certain meteorological and hydrological conditions such as calm weather and/or reduced current circulation (Franco and Michelato, 1992; Malej and Malačič, 1995) can trigger hypoxia/anoxia.

Oxygen depletions, often associated with massive marine snow events, have been noted here periodically for centuries (Crema et al., 1991), but their frequency and severity have markedly increased during recent decades. High anthropogenic input of nutrients into the Northern Adriatic (Justić et al., 1995; Danovaro, 2003; Druon et al., 2004) has led to a higher production and deposition of organic matter than there is oxygen supply to allow its decomposition (Rabalais and Turner, 2001; Bishop et al., 2006). The average long-term decrease in water body transparency here over the 20th century, accompanied by decreasing bottom oxygen concentrations since the 1950s, has been convincingly outlined by Justić (Justić et al., 1987; Justić, 1988). Since the 1980s, severe oxygen deficiencies have been reported here on a regular basis (e.g. Fedra et al., 1976; Stachowitsch, 1984; Hrs-Brenko et al., 1994; Penna et al., 2004). The impacted areas range from restricted areas (several km²;

Stachowitsch, 1992) to approx. 250 km² (Faganeli et al., 1985) to 4000 km² (Stefanon and Boldrin, 1982; D. Degobbis, pers. comm.), ultimately affecting every region (Fig. 1).

The Northern Adriatic is therefore a case study for recurring perturbations involving anoxia and marine snow events and shows profound effects on the species to community level (Šimunović et al., 1999; Barmawidjaja et al., 1995; Benović et al., 2000; Kollmann and Stachowitsch, 2001).

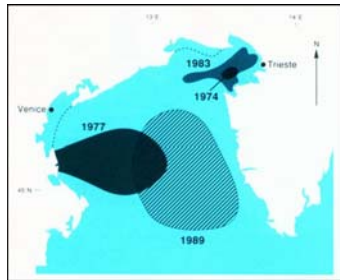


Figure 1. Bottom anoxias in the Northern Adriatic between 1974 and 1989. Virtually no area is unaffected and the number of unnoticed events is probably much higher (from Ott, 1992).

High-biomass suspension feeders and benthic control

Macroepifauna communities are widely distributed in the Northern Adriatic (Fedra, 1978; Zuschin et al., 1999) and largely consist of decimetre-scale, interspecific, high-biomass aggregations termed multi-species clumps (Fedra et al., 1976) or bioherms (Fig. 2): one or more shelly hard substrates provide the base for sessile, suspension-feeding colonizers (mostly sponges, ascidians, anemones or bivalves), which in turn serve as an elevated substrate for additional vagile and hemi-sessile organisms (mostly brittle stars and crabs) (Zuschin and Pervesler, 1996). The presence of a well-developed macroinfauna is expressed in the early designations (*Schizaster chiajei*-community) of the benthic communities here by Vatova (1949) and later authors (Gamulin-Brida, 1967; Orel and Menea, 1969; Orel et al., 1987; Occhipinti-Ambrogi et al., 2002).

The predominant, wide-ranging macroepibenthic community was named the ORM-community based on the biomass dominants, the brittle star *Ophiothrix quinquemaculata*, the sponge *Reniera* sp. and the ascidians *Microcosmus* spp. The mean biomass, measured as wet weight, amounted to 370 (± 73) g/m² (Fedra et al., 1976).

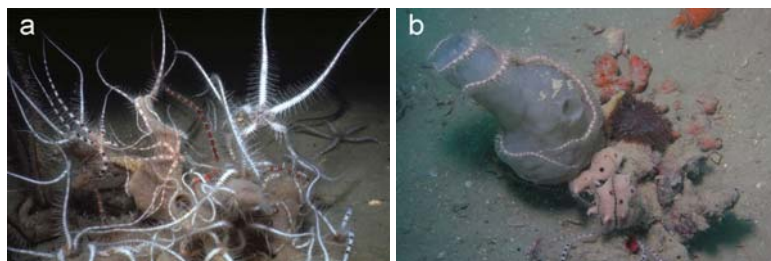


Figure 2. Typical aspect of ORM-community at 24 m depth, Gulf of Trieste. a) Dense aggregation of suspension-feeding brittle star *Ophiothrix quinquemaculata* on the sponge *Reniera* sp.; b) Multi-species clump, consisting of the ascidians *Phallusia mammilata* and *Microcosmus* spp., the sea anemone *Cereus pedunculatus*, various sponges, the sea cucumber *Ocnus planci* and *O. quinquemaculata*. [Photos: M. Stachowitsch and A. Haselmair].

In the shallow Northern Adriatic, the benthos is not merely a receiving compartment. Rather, complex feedback processes are in effect, with the benthic subsystem controlling and helping dampen oscillations in the pelagic subsystem (Ott, 1992). Ott and Fedra (1977) estimated that

the suspension feeders here can remove all the suspended material in the water column every 20 days. This is on the same order of magnitude as calculated for the Oosterschelde (Herman and Scholten, 1990), Swedish waters (Loo and Rosenberg, 1989), the USA (Cloern, 1982) and France (Hily, 1991). Such communities have therefore been termed a “natural eutrophication control” (Officer et al., 1982) and play a key role in the stability of the entire ecosystem.

The repeated low DO events, coupled with commercial fishing activities during recent decades, however, have led to the destruction of epifauna-based benthic communities in many areas (Stachowitsch and Fuchs, 1995; Kollmann and Stachowitsch, 2001; Fig. 3). Their loss makes the system more sensitive to perturbations. Other key functional processes for the overall system, such as bioturbation and related sedimentary activities, may also be altered by hypoxia/anoxia and the corresponding loss of biodiversity (Snelgrove, 1998; Rosenberg, 2001; Levin, 2002). The current status of the ORM-community makes it unlikely that it fully fulfils its pre-mortality regulatory capacity.

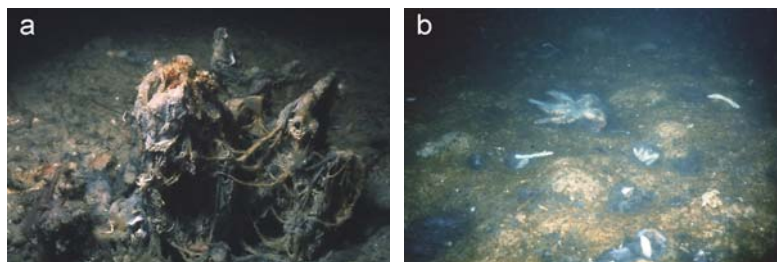


Figure 3. Mortality scenario after anoxia. a) Decomposing sponge bioherm with mucus cover and entangled crabs (*Pilumnus spinifer*, *Pisidia longicornis*); b) Typical late aspect of mass mortality. Decomposing sea star *Astropecten bispinosus* and sipunculids. Note lighter sediment mounds. [Photos: M. Stachowitsch].

Consequences on all levels

The point at which benthic animals are affected by low oxygen concentrations varies, but first indications of stress generally begin to appear when oxygen drops below 2.0-3.0 mg l⁻¹ (1.4-2.1 ml l⁻¹; Rabalais and Turner, 2001). Direct effects of exposure to hypoxia such as altered behaviour, physical inactivity and mass mortalities are well documented (Stachowitsch, 1984; Buzzelli et al., 2002; Montagna and Ritter, 2006). The larger, mobile benthos, for example, is often able to migrate out of the affected area, whereby the less mobile fauna – unable to escape or avoid hypoxic waters – exhibits a series of behavioural patterns in response to decreasing oxygen concentrations (Mistri, 2004). Infauna, for example, emerges from the sediment. Epifaunal organisms attempt to position themselves above the lowermost hypoxic bottom layer, either by moving onto higher substrates (Stachowitsch, 1991) or raising their bodies (i.e. arm-tipping brittle stars, siphon-stretching bivalves or tiptoeing crustaceans; reviewed by Diaz and Rosenberg, 1995).

Tolerance to hypoxia/anoxia in itself, however, is a question of physiological capacity and adaptability, which varies from species to species (Hagerman, 1998). Two “strategies”, depending on duration and intensity of the low oxygen bout, are possible. The first is to maintain aerobic respiration (e.g. increase in respiration rate, number of red blood cells, flow of blood through respiratory surfaces, or more effective use of respiratory pigments) as long as possible. The second is to resort to anaerobic respiration and reduce overall metabolism (e.g. resting, inactivity, down regulation of protein synthesis and certain regulatory enzymes) if severe hypoxia or anoxia prevails (Hagerman, 1998; Burnett and Stickle, 2001; Wu, 2002). However, once anaerobic conditions and H₂S develop, mass mortalities of nearly all organisms occur (Stachowitsch, 1984).

Diaz and Rosenberg (1995) reviewed the effects of hypoxia on benthic organisms. In general, fishes are more sensitive than crustaceans and echinoderms, whereby polychaetes and bivalves are the most tolerant. Within each taxon, however, there is considerable variability, dependent on the respective life habits (Gray et al. 2002).

In the Northern Adriatic, sea anemones are particularly tolerant to hypoxia due to a combination of physiological and behavioural adaptations (see Sassaman and Mangum, 1972; Shick, 1991). This is confirmed by other field and laboratory studies (Jørgensen, 1980; Wahl, 1984). In the 1983 mortality, for example, one week after the onset of the event, survivors predominantly included individual anthozoans such as *Ragactis pulchra*, *Cerianthus membranaceus* and *Epizoanthus erinaceus* (Stachowitsch, 1984). In our recent, artificially induced anoxia experiments in situ, *Cereus pedunculatus* was among the most tolerant species and survived more than 83 hours of anoxia and a final H₂S concentration of about 160 μM l⁻¹ (Riedel et al., in review). This information will be synthesized into a catalogue of behaviours, allowing indicator species to be defined and the status of benthic communities to be assessed.

Hypoxia may severely alter community composition by killing sensitive species but favouring a few tolerant forms (Dauer, 1993), and decreasing recruitment and growth (Breitburg 1992; Miller et al. 2002; Stierhoff et al. 2006). This will impact both the apparent and the potential biodiversity, e.g. pelagic resting stages in the sediment – important agents of local recolonization – will also be decimated (Boero and Bonsdorff, 2007; Danovaro and Pusceddu, 2007). Moreover, changes in functional types/groups (including ecosystem engineers; Crain and Bertness, 2006) occur along hypoxic gradients, influencing overall ecosystem properties (Pearson and Rosenberg, 1978; Diaz and Rosenberg, 1995): Suspension feeders might be replaced by deposit feeders, macrobenthos by meiobenthos, bioturbators may be lost, phytoplankton communities can become dominated by nanoplankton and microflagellates. The result is an unbalanced community dynamics, altering both function and composition in unforeseen ways (Grall and Chauvaud, 2002).

Beyond these direct effects, there is increasing evidence for indirect effects (Eby et al., 2005). These include altered competition and predator–prey interactions, whereby predation rates increase or decrease depending on the relative tolerances of predator and prey to anoxia (Breitburg et al., 1994; Sagasti et al., 2001; Decker et al., 2004; Riedel et al., 2008). Thus, hypoxia also affects the trophodynamics of marine ecosystems. Wu (2002) suggests a general shift from *K*-selected to *r*-selected species, and from complex to simple food chains.

Such scenarios, which are increasingly unfolding in shallow coastal waters around the world (Selman et al., 2008), represent undisputable worst-case situations for biodiversity and ecosystem function. The result is local extinction (Solan et al., 2004) and large-scale homogenization at the lowest possible level (Sala and Knowlton, 2006). The ultimate reflection will be a total loss of ecosystem services beyond the seas as navigational highways.

Climate change – adding insult to injury?

For the Mediterranean, many models predict a temperature increase by an average 3 °C until the end of the 21st century, with a larger warming in summer than the global average. Mean precipitation is expected to decrease, especially in summer, mainly due to the northward extension of the descending branch of the subtropical Hadley circulation (Li et al, 2006). However, future impacts on the coastal system will vary greatly at regional scales (Scavia et al., 2002). Clearly, the trends will be determined by complex interactions between temperature, precipitation, runoff, currents, salinity and wind.

Climate change will influence hypoxia/anoxia both directly and indirectly. The mechanism involves changes in coastal eutrophication by two major pathways (Fig. 4):

1) Temperature-related changes in atmospheric circulation patterns will alter hydrological cycles, leading to shifts in precipitation, evapotranspiration and subsequent changes in river quantity and quality regimes (Miller and Russell, 1992). Specifically, changes in the magnitude and seasonal patterns of freshwater and terrestrially derived nutrient inputs will profoundly affect coastal salinity, turbidity, water residence time and primary production (Justic et al., 2005; Harley et al. 2006). Prolonged residence times during low-flow conditions will promote algal blooms (Relexans et al. 1988), whereas storm-related high river flows result in higher nutrient inputs and stronger vertical salinity gradients. Both conditions favour the development of hypoxia/anoxia in bottom waters (Paerl et al. 1998; Scavia et al. 2002).

2) A warmer atmosphere leads to warmer water temperatures, which have a lower oxygen content available for respiration by aquatic organisms. Moreover, increased summertime surface temperatures, especially if coincident with reduced winds, will lead to more persistent stratification. This is a prerequisite for prolonged hypoxia/anoxia. (Justic et al. 2007; Thuiller, 2007). Finally, both photosynthesis and respiration are temperature-dependent processes and thus the rates of production, decomposition, and nutrient cycling are likely to increase (Kennedy et al. 2002; Harley et al. 2006).

In one of the few available models for the Northern Adriatic, Vichi et al (2003) predicted precisely such an overall enhancement of the water-column stratification on an annual basis, with stronger intensification during the summer. The diffusion of oxygen and nutrients between surface and bottom layers was reduced, and the transfer of organic matter through the food web shifted towards the smaller components of the microbial web.

Benthic and pelagic species will therefore be exposed to unusual temperature, salinity, and oxygen conditions. These factors will take most of the fauna to their physiological limits. Such stressed organisms, coupled with hypoxia-related denuded areas, will provide little resistance to disease and the immigration of alien species (Harvell et al., 2002; Osovitz and Hofmann, 2007).

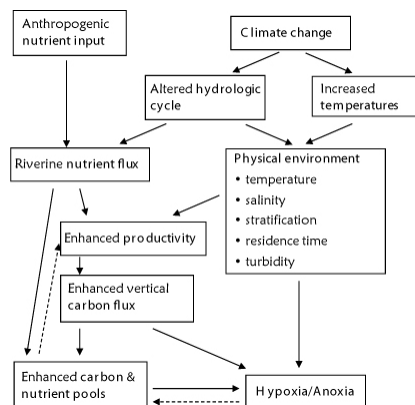


Figure 4. Coupling between climate variables and eutrophication. Possible pathways for the development of hypoxia and anoxia in shallow coastal areas. Broken arrows indicate feedback control (adapted from Justić et al., 2001; 2007).

Perspectives

Ecosystem stability is a crucial topic in modern ecology. In the Northern Adriatic, instability has been introduced by the recurring perturbations involving anoxia and marine snow events along with intensive dredging and trawling activities. Currently, the frequency of such disturbances greatly exceeds the duration of recolonization process. The situation in the Northern Adriatic has been described as “rapid death, slow recovery” (Stachowitsch, 1991).

Climate change is likely to affect hypoxia and anoxia in myriad ways and on different levels. Most of the anticipated changes will involve increased hypoxia/anoxia. Our current

research (Stachowitsch et al., 2007) on artificially induce oxygen depletion events on the sea floor – including time-lapse documentation – provides a foretaste of what mass mortality, biodiversity loss and local extinction here will look like (www.marine-hypoxia.com).

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