



Effects of natural and human-induced hypoxia on coastal benthos

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Coastal hypoxia (defined here as $<1.42 \text{ ml L}^{-1}$; $62.5 \text{ } \mu\text{M}$; 2 mg L^{-1} , approx. 30% oxygen saturation) develops seasonally in many estuaries, fjords, and along open coasts as a result of natural upwelling or from anthropogenic eutrophication induced by riverine nutrient inputs. Permanent hypoxia occurs naturally in some isolated seas and marine basins as well as in open slope oxygen minimum zones. Responses of benthos to hypoxia depend on the duration, predictability, and intensity of oxygen depletion and on whether H_2S is formed. Under suboxic conditions, large mats of filamentous sulfide oxidizing bacteria cover the seabed and consume sulfide. They are hypothesized to provide a detoxified microhabitat for eukaryotic benthic communities. Calcareous foraminiferans and nematodes are particularly tolerant of low oxygen concentrations and may attain high densities and dominance, often in association with microbial mats. When oxygen is sufficient to support metazoans, small, soft-bodied invertebrates (typically annelids), often with short generation times and elaborate branchial structures, predominate. Large taxa are more sensitive than small taxa to hypoxia. Crustaceans and echinoderms are typically more sensitive to hypoxia, with lower oxygen thresholds, than annelids, sipunculans, molluscs and cnidarians. Mobile fish and shellfish will migrate away from low-oxygen areas. Within a species, early life stages may be more subject to oxygen stress than older life stages. Hypoxia alters both the structure and function of benthic communities, but effects may differ with regional hypoxia history. Human-caused hypoxia is generally linked to eutrophication, and occurs adjacent to watersheds with large populations or agricultural activities. Many occurrences are seasonal, within estuaries, fjords or enclosed seas of the North Atlantic and the NW Pacific Oceans. Benthic faunal responses, elicited at oxygen levels below 2 ml L^{-1} , typically involve avoidance or mortality of large species and elevated abundances of enrichment opportunists, sometimes prior to population crashes. Areas of low oxygen persist seasonally or continuously beneath upwelling regions, associated with the upper parts of oxygen minimum zones (SE Pacific, W Africa, N Indian Ocean). These have a distribution largely distinct from eutrophic areas and support a resident fauna that is adapted to survive and reproduce at oxygen concentrations $<0.5 \text{ ml L}^{-1}$. Under both natural and eutrophication-caused hypoxia there is loss of diversity, through attrition of intolerant species and elevated dominance, as well as reductions in body size. These shifts in species composition and diversity yield altered trophic structure, energy flow pathways, and corresponding ecosystem services such as production, organic matter cycling and organic C burial. Increasingly the influences of nature and humans interact to generate or exacerbate hypoxia. A warmer ocean is more stratified, holds less oxygen, and may experience greater advection of oxygen-poor source waters, making new regions subject to hypoxia. Future understanding of benthic responses to hypoxia must be established in the context of global climate change and other human influences such as overfishing, pollution, disease, habitat loss, and species invasions.

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