

SIXTH FRAMEWORK PROGRAMME



Project contract no. 003933

THRESHOLDS **Thresholds of Environmental Sustainability** **INTEGRATED PROJECT**

Priority 1.1.6 "Sustainable Development, Global Change and Ecosystems"
Sub-Priority 1.1.6.3 "Global Change and Ecosystems"

<h3>Stream 5 – D5.3.2</h3> <p>Testing thresholds of hypoxia for various indicators of benthic macrofauna</p>
--

Due date of delivery:
Actual submission date:

Start date of project: 1st of January 2005

Duration: 48 months

Lead authors for this deliverable: [Raquel Vaquer (IMEDEA), Carlos M. Duarte (IMEDEA)]

Project co-funded by the European Commission within the Sixth Framework Programme (2002-2006)		
Dissemination Level		
PU	Public	
PP	Restricted to other programme participants (including the Commission Services)	
RE	Restricted to a group specified by the consortium (including the Commission Services)	
CO	Confidential, only for members of the consortium (including the Commission Services)	X

Table of Contents

EXECUTIVE SUMMARY	2
1. INTRODUCTION	3
2. METHODOLOGY	4
3. RESULTS	4
3.1 Sublethal thresholds on marine benthic communities	5
3.2 Median lethal concentration for marine benthic organisms	5
3.3 Median lethal time for marine benthic organisms	6
3.4 Factors affecting to thresholds of hypoxia for marine benthic organisms	6
4. CONCLUSIONS	8
5. REFERENCES	9

List of Figures

Figure 3.1 Cumulative distribution of oxygen thresholds for sublethal responses of marine benthic organisms (left panel) and its differences between taxonomic groups (right panel).....	5
Figure 3.2 Cumulative distribution of median lethal concentration for marine benthic organisms (left panel) and its differences between groups (right panel).....	6
Figure 3.3 Cumulative distribution of median lethal time for marine benthic organisms (left panel) and its differences between taxonomic groups.....	6
Figure 3.4 Median lethal time in hypoxia conditions vs. median lethal time in hypoxia and hydrogen sulphide for marine benthic organisms.....	7

Executive Summary

Hypoxia is a widespread problem affecting world's coastal and deep-sea waters with severe consequences on benthic communities, causing death and catastrophic changes. Hypoxia is linked to eutrophication and, as eutrophication, forecasted to increase in the future due to the combined effects of eutrophication and warming. We used a broad survey of the published literature to define the thresholds of hypoxia for sublethal and lethal responses of marine benthic communities. Specifically, we addressed the questions: (a) Is there a pattern in the successional sequence during oxygen depletion?; and (b) what are the thresholds of hypoxia for lethal and sublethal response of macrofauna species?, are there consistent differences across phyla?

1. Introduction

Events of low oxygen can cause serious problems in coastal areas of the world. Some of the severe consequences of hypoxic events include changes in populations of marine organisms such as large-scale mortality, as well as changes in biodiversity, changes in species distributions, physiological stress, and other sublethal effects, such as reduced growth and reproduction (Service, 2004).

Hypoxia in coastal areas is governed by physical and biogeochemical processes. Some of the potential causes of hypoxia in the coastal ocean include: enhanced delivery of nutrients and organic matter in areas with limited circulation and vertical mixing (strong water stratification and long water residence time); upwelling of deep oxygen-depleted waters near-coastal areas and subsequent warming; intrusions of deep waters rich nutrients (than can cause phytoplankton blooms). The combined effect of natural upwelling of low oxygen oceanic water and enhanced availability of nutrients and organic matter can accelerate and intensify coastal hypoxia.

Low oxygen conditions have important consequences in biogeochemical cycles and functioning of biological communities.

2. Methodology

A broad Literature search (Web of Science and Scholar Google) was used to assess the effects of hypoxia in marine benthic communities. From several thousand entries potentially relevant, about 200 papers with useful data were extracted as containing useful information. The data were extracted into a data set and all the units were standardized.

Compiling the negative effects of hypoxia in marine benthic organisms, most of the data available derived from experimental work in laboratories with individual species. Responses to hypoxia are often assessed from the survival or fraction of impacted populations with changes in O₂ concentration. The toxicity tests for which a broader empirical basis was found in the literature are:

-Sublethal thresholds (Median toxicity concentration): O₂ concentration conducive to the negative effects for 50% of the population.

-Median lethal concentration (LC50): Statistically-derived O₂ concentration at which 50% of the organisms in a given population die*.

-Median lethal time (LT50): Statistically-derived average time interval at which 50% of a given population may be expected to die following acute administration of a chemical or physical agent (O₂ in this case) at a given concentration under a defined set of conditions*.

*1993, 65, 2068. IUPAC Compendium of Chemical Terminology 2nd Edition (1997)

3. Results

The effects of hypoxia on benthic communities have been thoroughly reviewed by Díaz and Rosenberg (1995) and Gray et al. (2002). Hypoxia is conventionally defined as waters with oxygen concentrations < 2 mg O₂ L⁻¹ (Díaz and Rosenberg 1995, Díaz 2001). However, the vulnerability to low oxygen content varies greatly across marine organisms, so that the oxygen level at which sublethal and lethal hypoxic effects arise differ greatly across organisms. Indeed, a thorough review of the literature by Gray et al. (2002) concluded that many invertebrates already experience acute mortality at oxygen levels below 4 mg O₂ L⁻¹, with larval stages being, in general, more vulnerable than their corresponding adults (Gray et al. 2002). Fish appear to be the most vulnerable group to hypoxia, followed by crustaceans, annelids and bivalves, which are most tolerant (Gray et al. 2002). Most marine metazoans die at oxygen concentrations < 0.5 to 2.0 mg O₂ L⁻¹. Impacts of hypoxia on growth and behaviour are typically observed at higher oxygen concentrations of 4.5 to 6.0 mg O₂ L⁻¹, and other components of metabolism are affected between 2 and 4 mg O₂ L⁻¹ (Gray et al. 2002). Whereas fish can be expected to be able to avoid hypoxic waters, fish kills derive from hypoxia are, nevertheless, frequent (Paerl *et al.*, 1998, Rabalais *et al.*, 1994), suggesting that hypoxia often develops across spatial scales large enough and time scales fast enough as to preclude avoidance by mobile organisms. In addition, hypoxia often occurs along with other stresses, such as warm temperatures or metabolites of anaerobic metabolism, such as sulphide, enhancing the vulnerability of organisms to hypoxia relative to laboratory-derived estimates, typically based on manipulations of oxygen alone (Gray et al. 2002). Further, the length and frequency of hypoxic events affects the vulnerability of organisms, as it allows adaptive changes in the communities and species they contain. For instance, organisms present in fjords and bays with

restricted exchange where hypoxia maybe permanent appears to show higher critical oxygen concentrations than those in areas experiencing seasonal or shorter hypoxic events.

3.1 Sublethal thresholds on marine benthic communities.

Some negative effects of oxygen depletion on marine benthic organisms can be produced at higher oxygen content than that adopted in the conventional definition of hypoxia. These negative effects can affect the behaviour or the metabolism of the organisms.

In some fish larvae this sublethal thresholds can be met at 7 mg O₂/l for changes in their metabolism such as change in oxygen dependent metabolism or bradycardia sets.

From the data available in the literature the median oxygen content for sublethal effects on benthic organisms was $66.71 \pm 2.25 \mu\text{mol O}_2/\text{l}$ ($2.13 \pm 0.072 \text{ mg O}_2/\text{l}$). Half of the populations suffered negative effects with oxygen content lower than $89.25 \mu\text{mol O}_2/\text{l}$ ($2.8 \text{ mg O}_2/\text{l}$).

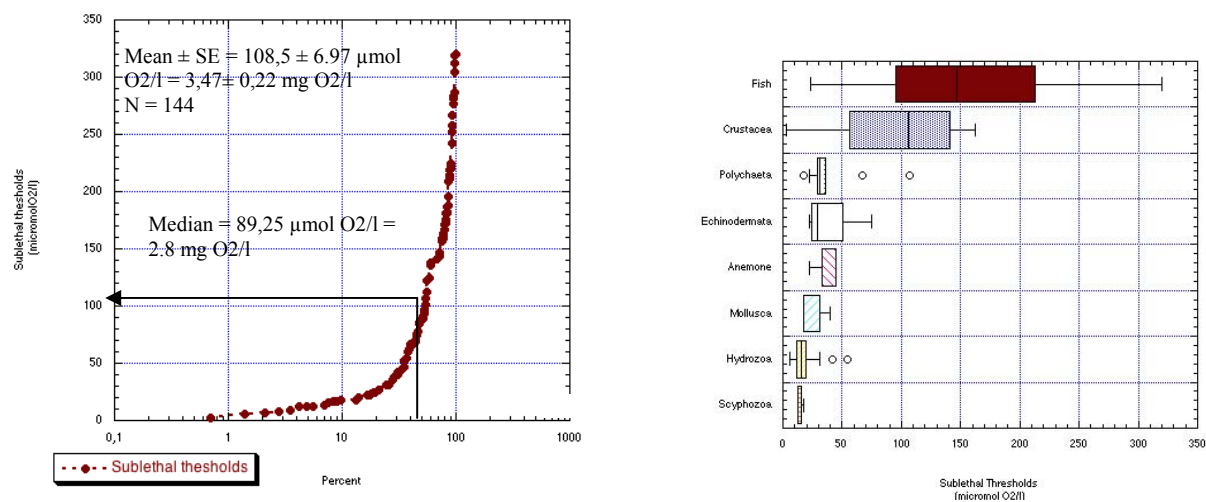


Figure 3.1 Cumulative distribution of oxygen thresholds for sublethal responses of marine benthic organisms (left panel) and its differences between taxonomic groups (right panel).

There are differences between taxonomic groups in the responses to oxygen depletion. Fish larvae are the most vulnerable to low level of oxygen content. Mobile organisms such as fishes can avoid hypoxic events swimming to areas with higher concentrations of oxygen. Crustaceans are the next taxonomic group in vulnerability to oxygen depletion. Polychaeta, echinodermata, anemone, mollusca, hydrozoa and scyphozoa are more tolerant to low oxygen concentrations.

3.2 Median lethal concentration for marine benthic organisms.

The average median lethal concentration for marine benthic organisms from the data compiled from the literature is $66.71 \pm 2.25 \mu\text{mol O}_2/\text{l}$ ($2.13 \pm 0.072 \text{ mg O}_2/\text{l}$). This oxygen content is higher than the conventional definition of hypoxia. The data belong to 265 different experiments that include 62 species.

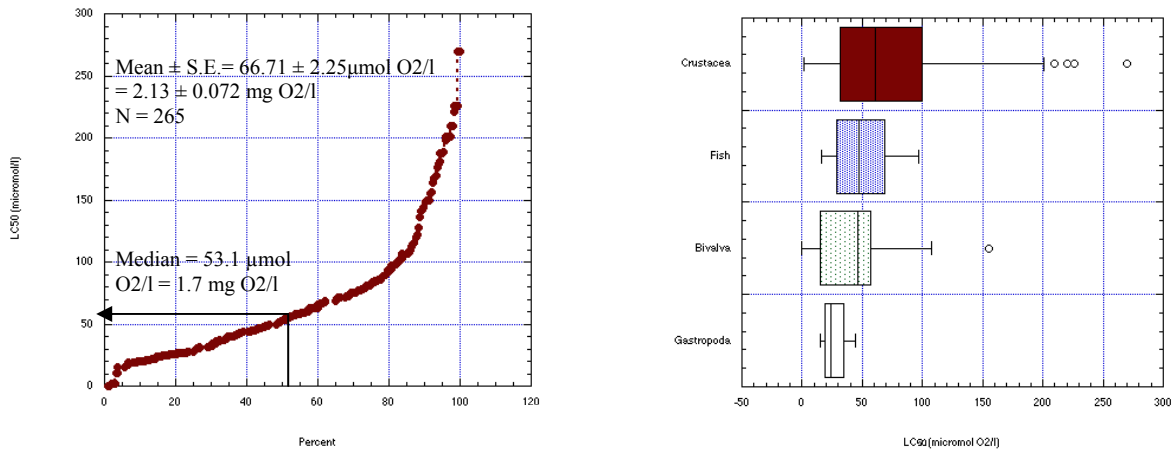


Figure 3.2 Cumulative distribution of median lethal concentration for marine benthic organisms (left panel) and its differences between groups (right panel).

The bigger amount of data available is from commercial species. In this case the most sensitive group is crustaceans, followed by fishes while the more resistant are molluscs.

3.3 Median lethal time for marine benthic organisms.

In water with oxygen content below to 2mg O₂/l a half of the tested organisms will die in the 119 hours following the exposure to this concentration.

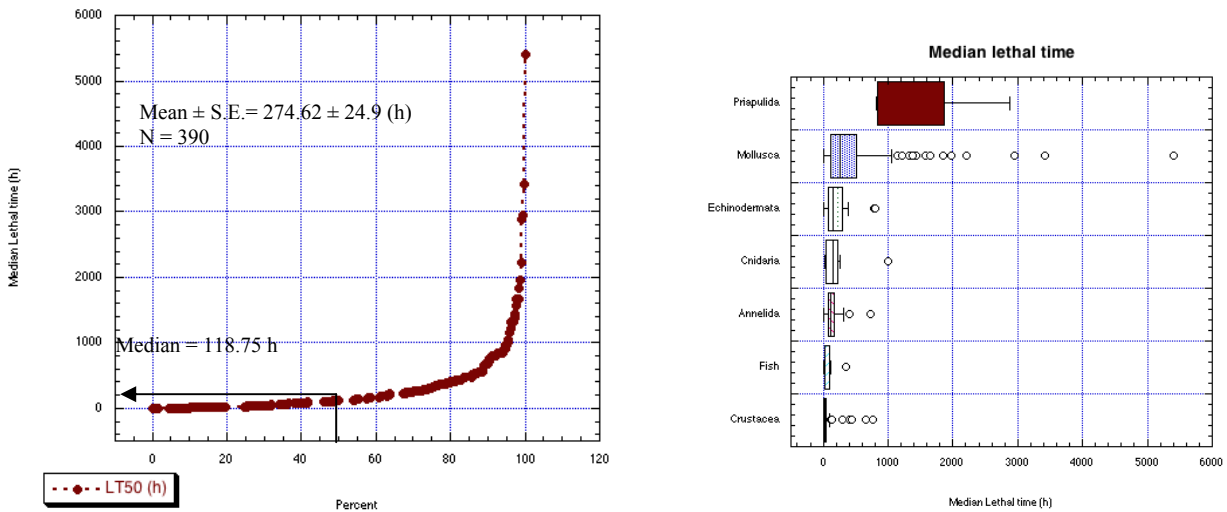


Figure 3.3 Cumulative distribution of median lethal time for marine benthic organisms (left panel) and its differences between taxonomic groups.

For median lethal time the most resistant group is priapulida that live in interstitial habitats, while the most sensitive are crustaceans.

3.4 Factors affecting to thresholds of hypoxia for marine benthic organisms.

Thresholds of hypoxia on benthic organisms are modulated by diverse factors. Some of them are dependent from the organism, like size, sex, life stage... Whereas others depend of the ambient, such as salinity, temperature, presence of hydrogen sulphide...

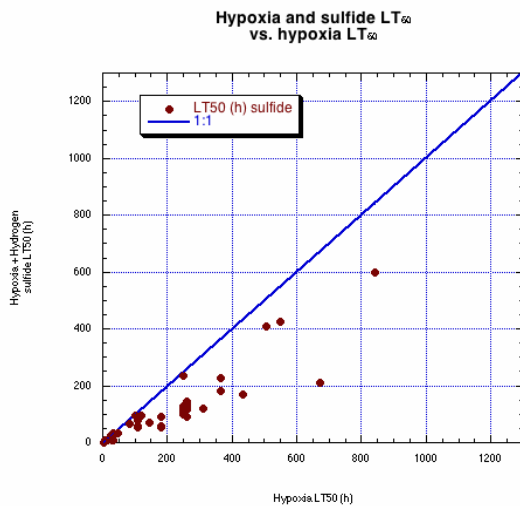


Figure 3.4 Median lethal time in hypoxia conditions vs. median lethal time in hypoxia and hydrogen sulphide for marine benthic organisms.

The presence of hydrogen sulphide reduces the median lethal time. The organism has to cope with hypoxia and with the negative effects of the presence of hydrogen sulphide.

Increases in temperature are also negative for the organisms that suffer low oxygen contents. Temperature is a key factor because is increasing with the climatic change and it increases the organism's metabolic rates. Increases in temperature are associated with decreases in the tolerance to hypoxia.

4. Conclusions

The conventional definition of hypoxia (2 mg/l) is below the precautionary limits for lethal thresholds, even below the average of median lethal concentration.

Precautionary limits for sublethal thresholds are 4.5-fold greater than traditionally definition of hypoxia.

Precautionary limits for median lethal concentration are 3-fold greater than traditionally definition of hypoxia.

The variability between groups is consistent with the succession of disappearance in the nature. While the fishes are the first group to avoid areas with oxygen depletion, the crustaceans are the most sensible group, followed by annelida, echinodermata and mollusca. The recolonization pattern is not the same pattern of disappearance. The first group in recolonize the depleted sediments are polichaeta, this is because recolonization was predominantly contributed by larval settlement rather than adult migration. Thresholds of hypoxia are modulated by diverse factors, some of the most important are the presence of sulphide and temperature increases.

5. References

- Aarset, A. V. and T. Aunaas (1990). "Metabolic Responses of the Sympagic Amphipods *Gammarus-Wilkitzkii* and *Onisimus-Glacialis* to Acute Temperature-Variations." *Marine Biology* 107(3): 433-438.
- Abeleoeschger, D., R. Oeschger, et al. (1994). "Biochemical Adaptations of *Nereis-Diversicolor* (Polychaeta) to Temporarily Increased Hydrogen-Peroxide Levels in Intertidal Sandflats." *Marine Ecology-Progress Series* 106(1-2): 101-110.
- Allan, G. L. and G. B. Maguire (1991). "Lethal Levels of Low Dissolved-Oxygen and Effects of Short-Term Oxygen Stress on Subsequent Growth of Juvenile *Penaeus-Monodon*." *Aquaculture* 94(1): 27-37.
- Anderson, S. J., R. J. A. Atkinson, et al. (1991). "Behavioral and Respiratory Adaptations of the Mud-Burrowing Shrimp *Calocaris-Macandreae* Bell (Thalassinidea, Crustacea) to the Burrow Environment." *Ophelia* 34(2): 143-156.
- Anderson, S. J., A. C. Taylor, et al. (1994). "Anaerobic Metabolism during Anoxia in the Burrowing Shrimp *Calocaris-Macandreae* Bell (Crustacea, Thalassinidea)." *Comparative Biochemistry and Physiology a-Physiology* 108(4): 515-522.
- Arntz, W. E. and H. Rumohr (1982). "An Experimental-Study of Macrobenthic Colonization and Succession, and the Importance of Seasonal-Variation in Temperate Latitudes." *Journal of Experimental Marine Biology and Ecology* 64(1): 17-45.
- Baker, S. M. and R. Mann (1994). "Description of Metamorphic Phases in the Oyster *Crassostrea-Virginica* and Effects of Hypoxia on Metamorphosis." *Marine Ecology-Progress Series* 104(1-2): 91-99.
- Bonsdorff, E., K. Aarnio, et al. (1991). "Temporal and Spatial Variability of Zoobenthic Communities in Archipelago Waters of the Northern Baltic Sea - Consequences of Eutrophication." *Internationale Revue Der Gesamten Hydrobiologie* 76(3): 433-449.
- Bonsdorff, E., R. J. Diaz, et al. (1996). "Characterization of soft-bottom benthic habitats of the Aland islands, northern Baltic sea." *Marine Ecology-Progress Series* 142(1-3): 235-245.
- Bonsdorff, E., A. O. Laine, et al. (2003). "Zoobenthos of the outer archipelago waters (N. Baltic Sea) - the importance of local conditions for spatial distribution patterns." *Boreal Environment Research* 8(2): 135-145.
- Borja, A., I. Muxika, et al. (2006). "Long-term recovery of soft-bottom benthos following urban and industrial sewage treatment in the Nervion estuary - (southern Bay of Biscay)." *Marine Ecology-Progress Series* 313: 43-55.

- Boutilier, R. G., T. G. West, et al. (2000). "The protective effects of hypoxia-induced hypometabolism in the Nautilus." *Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology* 170(4): 261-268.
- Breitburg, D. L., A. Adamack, et al. (2003). "The pattern and influence of low dissolved oxygen in the Patuxent River, a seasonally hypoxic estuary." *Estuaries* 26(2A): 280-297.
- Brooks, S. P. J., A. Dezwaan, et al. (1991). "Differential Survival of Venus-Gallina and Scapharca Inaequalis during Anoxic Stress - Covalent Modification of Phosphofructokinase and Glycogen-Phosphorylase during Anoxia." *Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology* 161(2): 207-212.
- Campbell, J. G. and L. R. Goodman (2004). "Acute sensitivity of juvenile shortnose sturgeon to low dissolved oxygen concentrations." *Transactions of the American Fisheries Society* 133(3): 772-776.
- Cerezo, J. and B. G. Garcia (2004). "The effects of oxygen levels on oxygen consumption, survival and ventilatory frequency of sharpnose sea bream (*Diplodus puntazzo* Gmelin, 1789) at different conditions of temperature and fish weight." *Journal of Applied Ichthyology* 20(6): 488-492.
- Cheng, S. Y., Y. H. Chang, et al. (2004). "Lethal levels of dissolved oxygen for *Haliotis diversicolor* supertexta at different salinity levels." *Journal of Shellfish Research* 23(2): 569-573.
- Christensen, A. B. and J. M. Colacino (2000). "Respiration in the burrowing brittlestar, *Hemipholis elongata* Say (Echinodermata, Ophiuroidea): a study of the effects of environmental variables on oxygen uptake." *Comparative Biochemistry and Physiology a-Molecular and Integrative Physiology* 127(2): 201-213.
- Condon, R. H., M. B. Decker, et al. (2001). "Effects of low dissolved oxygen on survival and asexual reproduction of scyphozoan polyps (*Chrysaora quinquecirrha*)." *Hydrobiologia* 451(1-3): 89-95.
- Conley D. J., H. C., Rahm L., Savchuk O.P., Wulff F. (2002). "Hypoxia in the Baltic Sea and Basin-scale Changes in Phosphorus Biochemistry." *Environmental Science & Technology* 36(24): 5315-5320.
- Connolly, N. M., M. R. Crossland, et al. (2004). "Effect of low dissolved oxygen on survival, emergence, and drift of tropical stream macroinvertebrates." *Journal of the North American Benthological Society* 23(2): 251-270.
- Cook, A. A., P. J. D. Lamshead, et al. (2000). "Nematode abundance at the oxygen minimum zone in the Arabian Sea." *Deep-Sea Research Part II-Topical Studies in Oceanography* 47(1-2): 75-85.
- Das, T. and W. B. Stickle (1993). "Sensitivity of Crabs *Callinectes Sapidus* and *C-Similis* and the Gastropod *Stramonita-Haemastoma* to Hypoxia and Anoxia." *Marine Ecology-Progress Series* 98(3): 263-274.
- Davis, J. (1975). "Minimal Dissolved Oxygen Requirements of Aquatic Life with Emphasis on Canadian Species: A Review " *Journal of the Fisheries Research Board of Canada* 32(12): 2295-2331.

- De Robertis, A., K. Eiane, et al. (2001). "Eat and run: anoxic feeding and subsequent aerobic recovery by *Orchomene obtusus* in Saanich Inlet, British Columbia, Canada." *Marine Ecology-Progress Series* 219: 221-227.
- de Zwaan, A., O. Cattani, et al. (2001). "Influence of incubation conditions on the anoxic survival of marine bivalves. Static and semi-static incubations." *Marine Ecology-Progress Series* 211: 169-179.
- DEAN, T. L. and J. RICHARDSON (1998). "Responses of seven species of native freshwater fish and a shrimp to low levels of dissolved oxygen." *New Zealand Journal of Marine and Freshwater Research*
- Desprez, M., H. Rybarczyk, et al. (1992). "Biological Impact of Eutrophication in the Bay of Somme and the Induction and Impact of Anoxia." *Netherlands Journal of Sea Research* 30: 149-159.
- Dezwaan, A., O. Cattani, et al. (1993). "Sulfide and Cyanide-Induced Mortality and Anaerobic Metabolism in the Arcid Blood Clam *Scapharca Inaequalis*." *Comparative Biochemistry and Physiology C-Pharmacology Toxicology & Endocrinology* 105(1): 49-54.
- Dezwaan, A., P. Cortesi, et al. (1995). "Resistance of Bivalves to Anoxia as a Response to Pollution-Induced Environmental-Stress." *Science of the Total Environment* 171(1-3): 121-125.
- Dezwaan, A., P. Cortesi, et al. (1991). "Differential Sensitivities to Hypoxia by 2 Anoxia-Tolerant Marine Mollusks - a Biochemical-Analysis." *Marine Biology* 111(3): 343-351.
- deZwaan, A. and R. H. M. Eertman (1996). "Anoxic or aerial survival of bivalves and other euryoxic invertebrates as a useful response to environmental stress - A comprehensive review." *Comparative Biochemistry and Physiology C-Pharmacology Toxicology & Endocrinology* 113(2): 299-312.
- Diaz, R. J. and R. Rosenberg (1995). "Marine benthic hypoxia: A review of its ecological effects and the behavioural responses of benthic macrofauna." *Oceanography and Marine Biology - an Annual Review*, Vol 33 33: 245-303.
- Diaz, R. J. (2001). "Overview of hypoxia around the world." *Journal of Environmental Quality* 30(2): 275-281.
- Diehl, W. J., L. McEdward, et al. (1979). "Response of *Luidia-Clathrata* (Echinodermata, Asteroidea) to Hypoxia." *Comparative Biochemistry and Physiology a-Physiology* 62(3): 669-671.
- Dries, R. R. and H. Theede (1974). "Resistance to Oxygen Deficiency in Marine Bottom Invertebrates of Western Baltic Sea." *Marine Biology* 25(4): 327-333.
- Duineveld, G. C. A., P. De Wilde, et al. (1997). "Benthic respiration and standing stock on two contrasting continental margins in the western Indian Ocean: the Yemen-Somali upwelling region and the margin off Kenya." *Deep-Sea Research Part II-Topical Studies in Oceanography* 44(6-7): 1293-1317.
- Eden, N., T. Katz, et al. (2003). "Dynamic response of a mud snail *Nassarius sinusigerus* to changes in sediment biogeochemistry." *Marine Ecology-Progress Series* 263: 139-147.

- Engle, V. D., J. K. Summers, et al. (1999). "Dissolved oxygen conditions in northern Gulf of Mexico estuaries." *Environmental Monitoring and Assessment* 57(1): 1-20.
- Flemer D.A., W. L. K., Barbara F. Ruth & Charles M. Bundrick (1999). "The relative influence of hypoxia, anoxia, and associated environmental factors as determinants of macrobenthic community structure in a Northern Gulf of Mexico estuary." *Journal of Aquatic Ecosystem Stress and Recovery* 6(4): 311-328.
- Gallardo, V. A., M. Palma, et al. (2004). "Macrobenthic zonation caused by the oxygen minimum zone on the shelf and slope off central Chile." *Deep-Sea Research Part Ii-Topical Studies in Oceanography* 51(20-21): 2475-2490.
- Gamble, J. C. (1970). "Anaerobic Survival of Crustaceans *Corophium-Volutator*, *C-Arenarium* and *Tanais-Chevreuxi*." *Journal of the Marine Biological Association of the United Kingdom* 50(3): 657-&.
- Giere, O., J. H. Preusse, et al. (1999). "Tubificoides benedii (Tubificidae, Oligochaeta) - a pioneer in hypoxic and sulfidic environments. An overview of adaptive pathways." *Hydrobiologia* 406: 235-241.
- Gonzalez-Oreja, J. A. and J. I. Saiz-Salinas (1998). "Exploring the relationships between abiotic variables and benthic community structure in a polluted estuarine system." *Water Research* 32(12): 3799-3807.
- Grantham, B. A., F. Chan, et al. (2004). "Upwelling-driven nearshore hypoxia signals ecosystem and oceanographic changes in the northeast Pacific." *Nature* 429(6993): 749-754.
- Gray, J. S., R. S. S. Wu, et al. (2002). "Effects of hypoxia and organic enrichment on the coastal marine environment." *Marine Ecology-Progress Series* 238: 249-279.
- Greve, T. M., J. Borum, et al. (2003). "Meristematic oxygen variability in eelgrass (*Zostera marina*)." *Limnology and Oceanography* 48(1): 210-216.
- Gunter, G., F. G. W. Smith, et al. (1947). "Mass Mortality of Marine Animals on the Lower West Coast of Florida, November 1946-January 1947." *Science* 105(2723): 256-257.
- Gunter, G., R. H. Williams, et al. (1948). "Catastrophic Mass Mortality of Marine Animals and Coincident Phytoplankton Bloom on the West Coast of Florida, November 1946 to August 1947." *Ecological Monographs* 18(3): 309-324.
- Hagerman, L. and B. Vismann (1995). "Anaerobic Metabolism in the Shrimp Crangon-Crangon Exposed to Hypoxia, Anoxia and Hydrogen-Sulfide." *Marine Biology* 123(2): 235-240.
- Helly, J. J. and L. A. Levin (2004). "Global distribution of naturally occurring marine hypoxia on continental margins." *Deep-Sea Research Part I-Oceanographic Research Papers* 51(9): 1159-1168.

- Herreid, C. F. (1980). "Hypoxia in Invertebrates." *Comparative Biochemistry and Physiology a-Physiology* 67(3): 311-320.
- Hoback, W. W. and M. C. Barnhart (1996). "Lethal limits and sublethal effects of hypoxia on the amphipod *Gammarus pseudolimnaeus*." *Journal of the North American Benthological Society* 15(1): 117-126.
- Holte, B., E. Oug, et al. (2005). "Soft-bottom fauna and oxygen minima in sub-arctic north Norwegian marine sill basins." *Marine Biology Research* 1(2): 85-96.
- Irving, E. C., K. Liber, et al. (2004). "Lethal and sublethal effects of low dissolved oxygen condition on two aquatic invertebrates, *Chironomus tentans* and *Hyaella azteca*." *Environmental Toxicology and Chemistry* 23(6): 1561-1566.
- Irwin, S., V. Wall, et al. (2007). "Measurement of temperature and salinity effects on oxygen consumption of *Artemia franciscana* K., measured using fibre-optic oxygen microsensors." *Hydrobiologia* 575: 109-115.
- Ishibashi, Y., K. Inoue, et al. (2005). "Ontogeny of tolerance to hypoxia and oxygen consumption of larval and juvenile red sea bream, *Pagrus major*." *Aquaculture* 244(1-4): 331-340.
- Jahn, A. and H. Theede (1997). "Different degrees of tolerance to hydrogen sulphide in populations of *Macoma balthica* (Bivalvia, Tellinidae)." *Marine Ecology-Progress Series* 154: 185-196.
- Johansson, B. (1997). "Tolerance of the deposit-feeding Baltic amphipods *Monoporeia affinis* and *Pontoporeia femorata* to oxygen deficiency." *Marine Ecology-Progress Series* 151(1-3): 135-141.
- Johansson, B. (1999). "Influence of oxygen levels on the predatory behaviour of the isopod *Saduria entomon*." *Marine and Freshwater Behaviour and Physiology* 32(4): 223-238.
- Johns, A. R., A. C. Taylor, et al. (1997). "Sulphide metabolism in Thalassinidean Crustacea." *Journal of the Marine Biological Association of the United Kingdom* 77(1): 127-144.
- Johnson, P. D. and R. F. McMahon (1998). "Effects of temperature and chronic hypoxia on survivorship of the zebra mussel (*Dreissena polymorpha*) and Asian clam (*Corbicula fluminea*)." *Canadian Journal of Fisheries and Aquatic Sciences* 55(7): 1564-1572.
- Jorgensen, B. B. (1980). "Seasonal Oxygen Depletion in the Bottom Waters of a Danish Fjord and Its Effect on the Benthic Community." *Oikos* 34(1): 68-76.
- Karlson, K., R. Rosenberg, et al. (2002). "Temporal and spatial large-scale effects of eutrophication and oxygen deficiency on benthic fauna in Scandinavian and Baltic waters - A review." *Oceanography and Marine Biology*, Vol 40 40: 427-489.
- Keckeis, H., E. Bauer-Nemeschkal, et al. (1996). "Effects of reduced oxygen level on the mortality and hatching rate of *Chondrostoma nasus* embryos." *Journal of Fish Biology* 49(3): 430-440.

- Krang, A. S. and G. Rosenqvist (2006). "Effects of manganese on chemically induced food search behaviour of the Norway lobster, *Nephrops norvegicus* (L.)." *Aquatic Toxicology* 78(3): 284-291.
- Kristensen, E. (1983). "Ventilation and Oxygen-Uptake by 3 Species of *Nereis* (Annelida, Polychaeta) .1. Effects of Hypoxia." *Marine Ecology-Progress Series* 12(3): 289-297.
- Kristensen, E. (1983). "Ventilation and Oxygen-Uptake by 3 Species of *Nereis* (Annelida, Polychaeta) .2. Effects of Temperature and Salinity Changes." *Marine Ecology-Progress Series* 12(3): 299-305.
- Laudien, J., D. Schiedek, et al. (2002). "Survivorship of juvenile surf clams *Donax serra* (Bivalvia, Donacidae) exposed to severe hypoxia and hydrogen sulphide." *Journal of Experimental Marine Biology and Ecology* 271(1): 9-23.
- Levin, L., D. Gutierrez, et al. (2002). "Benthic processes on the Peru margin: a transect across the oxygen minimum zone during the 1997-98 El Nino." *Progress in Oceanography* 53(1): 1-27.
- Levin, L. A. (2003). "Oxygen minimum zone benthos: Adaptation and community response to hypoxia." *Oceanography and Marine Biology*, Vol 41 41: 1-45.
- Levin, L. A., S. E. Childers, et al. (1991). "Epibenthic, Agglutinating Foraminiferans in the Santa-Catalina Basin and Their Response to Disturbance." *Deep-Sea Research Part a-Oceanographic Research Papers* 38(4): 465-483.
- Levin, L. A. and J. D. Gage (1998). "Relationships between oxygen, organic matter and the diversity of bathyal macrofauna." *Deep-Sea Research Part Ii-Topical Studies in Oceanography* 45(1-3): 129-163.
- Levin, L. A., J. D. Gage, et al. (2000). "Macrobenthic community structure within and beneath the oxygen minimum zone, NW Arabian Sea." *Deep-Sea Research Part Ii-Topical Studies in Oceanography* 47(1-2): 189-226.
- Levin, L. A., C. L. Huggett, et al. (1991). "Control of Deep-Sea Benthic Community Structure by Oxygen and Organic-Matter Gradients in the Eastern Pacific-Ocean." *Journal of Marine Research* 49(4): 763-800.
- Levin, L. A., A. E. Rathburn, et al. (2003). "Bioturbation by symbiont-bearing annelids in near-anoxic sediments: Implications for biofacies models and paleo-oxygen assessments." *Palaeogeography Palaeoclimatology Palaeoecology* 199(1-2): 129-140.
- Levin, L. A., A. E. Rathburn, et al. (2004). "Bioturbation by symbiont-bearing annelids in near-anoxic sediments: Implications for biofacies models and paleo-oxygen assessments (vol 199, pg 129, 2003)." *Palaeogeography Palaeoclimatology Palaeoecology* 203(3-4): 347-348.
- Levitt, J. M. and A. J. Arp (1991). "The Effects of Sulfide on the Anaerobic Metabolism of 2 Congeneric Species of Mudflat Clams." *Comparative Biochemistry and Physiology B-Biochemistry & Molecular Biology* 98(2-3): 339-347.

- Llanso, R. J. (1991). "Tolerance of Low Dissolved-Oxygen and Hydrogen-Sulfide by the Polychaete *Streblospio-Benedicti* (Webster)." *Journal of Experimental Marine Biology and Ecology* 153(2): 165-178.
- Llanso, R. J. and R. J. Diaz (1994). "Tolerance to Low Dissolved-Oxygen by the Tubicolous Polychaete *Loimia-Medusa*." *Journal of the Marine Biological Association of the United Kingdom* 74(1): 143-148.
- Lu, L. and R. S. S. Wu (2000). "An experimental study on recolonization and succession of marine macrobenthos in defaunated sediment." *Marine Biology* 136(2): 291-302.
- MacKay, R. D. (1974). "A note on minimal levels of oxygen required to maintain life in *Penaeus schmitti*." *Journal of Mariculture Society* 5: 451-452.
- Mallin, M. A., M. R. McIver, et al. (2005). "Reversal of eutrophication following sewage treatment upgrades in the New River Estuary, North Carolina." *Estuaries* 28(5): 750-760.
- Marcus, N. H. and R. V. Lutz (1994). "Effects of Anoxia on the Viability of Subitaneous Eggs of Planktonic Copepods." *Marine Biology* 121(1): 83-87.
- Marcus, N. H., R. V. Lutz, et al. (1997). "Impact of anoxia and sulfide on the viability of eggs of three planktonic copepods." *Marine Ecology-Progress Series* 146(1-3): 291-295.
- Marcus, N. H., C. Richmond, et al. (2004). "Impact of hypoxia on the survival, egg production and population dynamics of *Acartia tonsa* Dana." *Journal of Experimental Marine Biology and Ecology* 301(2): 111-128.
- Martinez, E., M. Aguilar, et al. (1998). "Lethal low dissolved oxygen concentrations for postlarvae and early juvenile *Penaeus setiferus* at different salinities and pH." *Journal of the World Aquaculture Society* 29(2): 221-229.
- Matthews, M. A. and R. F. McMahon (1999). "Effects of temperature and temperature acclimation on survival of zebra mussels (*Dreissena polymorpha*) and Asian clams (*Corbicula fluminea*) under extreme hypoxia." *Journal of Molluscan Studies* 65: 317-325.
- Miller, D. C., S. L. Poucher, et al. (2002). "Determination of lethal dissolved oxygen levels for selected marine and estuarine fishes, crustaceans, and a bivalve." *Marine Biology* 140(2): 287-296.
- Moodley, L., C. H. R. Heip, et al. (1998). "Benthic activity in sediments of the northwestern Adriatic Sea: sediment oxygen consumption, macro- and meiofauna dynamics." *Journal of Sea Research* 40(3-4): 263-280.
- Moodley, L., G. J. vanderZwaan, et al. (1997). "Differential response of benthic meiofauna to anoxia with special reference to Foraminifera (Protista: Sarcodina)." *Marine Ecology-Progress Series* 158: 151-163.

- Naqvi, S. W. A., D. A. Jayakumar, et al. (2000). "Increased marine production of N₂O due to intensifying anoxia on the Indian continental shelf." *Nature* 408(6810): 346-349.
- Nielsen, A. and L. Hagerman (1998). "Effects of short-term hypoxia on metabolism and haemocyanin oxygen transport in the prawns *Palaemon adspersus* and *Palaemonetes varians*." *Marine Ecology-Progress Series* 167: 177-183.
- Nilsson, H. C. and R. Rosenberg (1994). "Hypoxic Response of 2 Marine Benthic Communities." *Marine Ecology-Progress Series* 115(3): 209-217.
- Nodder, S. D., C. A. Pilditch, et al. (2003). "Variability in benthic biomass and activity beneath the subtropical front, Chatham Rise, SW Pacific Ocean." *Deep-Sea Research Part I-Oceanographic Research Papers* 50(8): 959-985.
- Norkko, A. and E. Bonsdorff (1996). "Rapid zoobenthic community responses to accumulations of drifting algae." *Marine Ecology-Progress Series* 131(1-3): 143-157.
- Normant, M. and A. Szaniawska (2000). "Behaviour, survival and glycogen utilisation in the Baltic isopod *Saduria entomon* exposed to long-term oxygen depletion." *Marine and Freshwater Behaviour and Physiology* 33(3): 201-211.
- Paerl, H. W., J. L. Pinckney, et al. (1998). "Ecosystem responses to internal and watershed organic matter loading: consequences for hypoxia in the eutrophying Neuse river estuary, North Carolina, USA." *Marine Ecology-Progress Series* 166: 17-25.
- Paerl, H. W. (2006). "Assessing and managing nutrient-enhanced eutrophication in estuarine and coastal waters: Interactive effects of human and climatic perturbations." *Ecological Engineering* 26(1): 40-54.
- Palma, M., E. Quiroga, et al. (2005). "Macrobenthic animal assemblages of the continental margin off Chile (22 degrees to 42 degrees S)." *Journal of the Marine Biological Association of the United Kingdom* 85(2): 233-245.
- Perus, J. and E. Bonsdorff (2004). "Long-term changes in macrozoobenthos in the Aland archipelago, northern Baltic Sea." *Journal of Sea Research* 52(1): 45-56.
- Plante, S., D. Chabot, et al. (1998). "Hypoxia tolerance in Atlantic cod." *Journal of Fish Biology* 53(6): 1342-1356.
- Quiroga, E., R. Quinones, et al. (2005). "Biomass size-spectra of macrobenthic communities in the oxygen minimum zone off Chile." *Estuarine Coastal and Shelf Science* 62(1-2): 217-231.
- Rabalais, N. N., W. J. Wiseman, et al. (1994). "Comparison of Continuous Records of near-Bottom Dissolved-Oxygen from the Hypoxia Zone Along the Louisiana Coast." *Estuaries* 17(4): 850-861.
- Rabalais, N. N., R. E. Turner, et al. (2001). "Hypoxia in the Gulf of Mexico." *Journal of Environmental Quality* 30(2): 320-329.

- Ritter, C. and P. A. Montagna (1999). "Seasonal hypoxia and models of benthic response in a Texas bay." *Estuaries* 22(1): 7-20.
- Rosas, C., N. Lopez, et al. (2001). "Effect of salinity acclimation on oxygen consumption of juveniles of the white shrimp *Litopenaeus vannamei*." *Journal of Crustacean Biology* 21(4): 912-922.
- Rosas, C., E. Martinez, et al. (1998). "Effect of dissolved oxygen on the energy balance and survival of *Penaeus setiferus* juveniles." *Marine Ecology-Progress Series* 174: 67-75.
- Rosas, C., E. Martinez, et al. (1999). "The effect of dissolved oxygen and salinity on oxygen consumption, ammonia excretion and osmotic pressure of *Penaeus setiferus* (Linnaeus) juveniles." *Journal of Experimental Marine Biology and Ecology* 234(1): 41-57.
- Rosas, C., A. Sanchez, et al. (1997). "Critical dissolved oxygen level to *Penaeus setiferus* and *Penaeus schmitti* postlarvae (PL10-18) exposed to salinity changes." *Aquaculture* 152(1-4): 259-272.
- Rosenberg, R. (1976). "Benthic Faunal Dynamics during Succession Following Pollution Abatement in a Swedish Estuary." *Oikos* 27(3): 414-427.
- Rosenberg, R. (2001). "Marine benthic faunal successional stages and related sedimentary activity." *Scientia Marina* 65: 107-119.
- Rosenberg, R., S. Agrenius, et al. (2002). "Recovery of marine benthic habitats and fauna in a Swedish fjord following improved oxygen conditions." *Marine Ecology-Progress Series* 234: 43-53.
- Rosenberg, R., W. E. Arntz, et al. (1983). "Benthos Biomass and Oxygen Deficiency in the Upwelling System Off Peru." *Journal of Marine Research* 41(2): 263-279.
- Rosenberg, R., L. O. Loo, et al. (1992). "Hypoxia, Salinity and Temperature as Structuring Factors for Marine Benthic Communities in a Eutrophic Area." *Netherlands Journal of Sea Research* 30: 121-129.
- Rosenberg, R., H. C. Nilsson, et al. (2001). "Response of benthic fauna and changing sediment redox profiles over a hypoxic gradient." *Estuarine Coastal and Shelf Science* 53(3): 343-350.
- Rowe, G. T., M. E. C. Kaegi, et al. (2002). "Sediment community metabolism associated with continental shelf hypoxia, Northern Gulf of Mexico." *Estuaries* 25(6A): 1097-1106.
- Rutherford, L. D. and E. V. Thuesen (2005). "Metabolic performance and survival of medusae in estuarine hypoxia." *Marine Ecology-Progress Series* 294: 189-200.
- Sagasti, A., L. C. Schaffner, et al. (2001). "Effects of periodic hypoxia on mortality, feeding and predation in an estuarine epifaunal community." *Journal of Experimental Marine Biology and Ecology* 258(2): 257-283.
- Sandberg, E. (1994). "Does Short-Term Oxygen Depletion Affect Predator-Prey Relationships in Zoobenthos - Experiments with the Isopod *Saduria Entomon*." *Marine Ecology-Progress Series* 103(1-2): 73-80.

- Scavia, D., J. C. Field, et al. (2002). "Climate change impacts on US coastal and marine ecosystems." *Estuaries* 25(2): 149-164.
- Schottler, U. and M. Grieshaber (1988). "Adaptation of the Polychaete Worm *Scoloplos-Armiger* to Hypoxic Conditions." *Marine Biology* 99(2): 215-222.
- Schurmann, H. and J. F. Steffensen (1992). "Lethal Oxygen Levels at Different Temperatures and the Preferred Temperature during Hypoxia of the Atlantic Cod, *Gadus-Morhua* L." *Journal of Fish Biology* 41(6): 927-934.
- Seibel, B. A. and J. J. Childress (2000). "Metabolism of benthic octopods (Cephalopoda) as a function of habitat depth and oxygen concentration." *Deep-Sea Research Part I-Oceanographic Research Papers* 47(7): 1247-1260.
- Seidman, E. R. and A. L. Lawrence (1985). "Growth, feed digestibility, and proximate body composition of juvenile *Penaeus vannamei* and *Penaeus monodon* grown at different dissolved oxygen levels." *World Mariculture Society* 16: 333-346.
- Service, R. F. (2004). "Oceanography - New dead zone off Oregon coast hints at sea change in currents." *Science* 305(5687): 1099-1099.
- Shick, J. M. (1976). "Physiological and Behavioral-Responses to Hypoxia and Hydrogen-Sulfide in Infaunal Asteroid *Ctenodiscus-Crispatus*." *Marine Biology* 37(3): 279-289.
- Shumway, S. E., T. M. Scott, et al. (1983). "The Effects of Anoxia and Hydrogen-Sulfide on Survival, Activity and Metabolic-Rate in the Coot Clam, *Mulinia-Lateralis* (Say)." *Journal of Experimental Marine Biology and Ecology* 71(2): 135-146.
- Soltwedel, T., D. Portnova, et al. (2005). "The small-sized benthic biota of the Hakon Mosby Mud Volcano (SW Barents Sea slope)." *Journal of Marine Systems* 55(3-4): 271-290.
- Spanopoulos-Hernandez, M., C. A. Martinez-Palacios, et al. (2005). "The combined effects of salinity and temperature on the oxygen consumption of juvenile shrimps *Litopenaeus stylirostris* (Stimpson, 1874)." *Aquaculture* 244(1-4): 341-348.
- Staples, J. F., J. J. Hershkowitz, et al. (2000). "Effects of ambient PO₂ and temperature on oxygen uptake in *Nautilus pompilius*." *Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology* 170(3): 231-236.
- Steimle, F. W. and C. J. Sindermann (1978). "Review of Oxygen Depletion and Associated Mass Mortalities of Shellfish in the Middle Atlantic Bight in 1976." *Marine Fisheries Review* 40(12): 17-26.
- Stickle, W. B., M. A. Kapper, et al. (1989). "Metabolic Adaptations of Several Species of Crustaceans and Mollusks to Hypoxia - Tolerance and Microcalorimetric Studies." *Biological Bulletin* 177(2): 303-312.

- Tallqvist, M., E. Sandberg-Kilpi, et al. (1999). "Juvenile flounder, *Platichthys flesus* (L.), under hypoxia: effects on tolerance, ventilation rate and predation efficiency." *Journal of Experimental Marine Biology and Ecology* 242(1): 75-93.
- Tamai, K. (1993). "Tolerance of *Theora-Fragilis* (Bivalvia, Semelidae) to Low Concentrations of Dissolved-Oxygen." *Nippon Suisan Gakkaishi* 59(4): 615-620.
- Tamai, K. (1996). "Temporal tolerance of larval *Theora fragilis* (Bivalvia: Semelidae) to hypoxic conditions." *Fisheries Science* 62(6): 996-997.
- Tamburri, M. N., K. Wasson, et al. (2002). "Ballast water deoxygenation can prevent aquatic introductions while reducing ship corrosion." *Biological Conservation* 103(3): 331-341.
- Tankersley, R. A. and M. G. Wieber (2000). "Physiological responses of postlarval and juvenile blue crabs *Callinectes sapidus* to hypoxia and anoxia." *Marine Ecology-Progress Series* 194: 179-191.
- Taylor, A. C. and A. R. Brand (1975). "Effects of Hypoxia and Body Size on Oxygen-Consumption of Bivalve *Arctica-Islandica* (L)." *Journal of Experimental Marine Biology and Ecology* 19(2): 187-196.
- Taylor, J. C. and J. M. Miller (2001). "Physiological performance of juvenile southern flounder, *Paralichthys lethostigma* (Jordan and Gilbert, 1884), in chronic and episodic hypoxia." *Journal of Experimental Marine Biology and Ecology* 258(2): 195-214.
- Theede, H., A. Ponat, et al. (1969). "Studies on Resistance of Marine Bottom Invertebrates to Oxygen-Deficiency and Hydrogen Sulphide." *Marine Biology* 2(4): 325-&.
- Thuesen, E. V., L. D. Rutherford, et al. (2005). "Intragel oxygen promotes hypoxia tolerance of scyphomedusae." *Journal of Experimental Biology* 208(13): 2475-2482.
- Torrentera, L. and S. I. Dodson (2004). "Ecology of the brine shrimp *Artemia* in the Yucatan, Mexico, Salterns." *Journal of Plankton Research* 26(6): 617-624.
- Travizi, A. (2000). "Effect of anoxic stress on density and distribution of sediment meiofauna." *Periodicum Biologorum* 102(2): 207-215.
- Valverde, J. C. and B. G. Garcia (2005). "Suitable dissolved oxygen levels for common octopus (*Octopus vulgaris* Cuvier, 1797) at different weights and temperatures: analysis of respiratory behaviour." *Aquaculture* 244(1-4): 303-314.
- van den Thillart, G., R. Y. George, et al. (1999). "Hypoxia sensitivity and respiration of the euphausiid crustacean *Meganyctiphanes norvegica* from Gullmar Fjord, Sweden." *Sarsia* 84(2): 105-109.
- Vandenthillart, G., G. Vanlieshout, et al. (1992). "Influence of Long-Term Hypoxia on the Energy-Metabolism of the Hemoglobin-Containing Bivalve *Scapharca-Inaequalis* - Critical O₂ Levels for Metabolic Depression." *Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology* 162(4): 297-304.

- Vargo, S. L. and A. N. Sastry (1977). "Acute Temperature and Low Dissolved-Oxygen Tolerances of Brachyuran Crab (*Cancer-Irroratus*) Larvae." *Marine Biology* 40(2): 165-171.
- Vetter, R. A. H., H. D. Franke, et al. (1999). "Habitat-related differences in the responses to oxygen deficiencies in *Idotea baltica* and *Idotea emarginata* (Isopoda, Crustacea)." *Journal of Experimental Marine Biology and Ecology* 239(2): 259-272.
- Vistisen, B. and B. Vismann (1997). "Tolerance to low oxygen and sulfide in *Amphiura filiformis* and *Ophiura albida* (Echinodermata: Ophiuroidea)." *Marine Biology* 128(2): 241-246.
- Vopel, K., J. Dehmlow, et al. (1998). "Effects of anoxia and sulphide on populations of *Cletocamptus confluens* (Copepoda, Harpacticoida)." *Marine Ecology-Progress Series* 175: 121-128.
- Wang, W. X. and J. Widdows (1991). "Physiological-Responses of Mussel Larvae *Mytilus-Edulis* to Environmental Hypoxia and Anoxia." *Marine Ecology-Progress Series* 70(3): 223-236.
- Weeks, S. J., B. Currie, et al. (2002). "Satellite imaging - Massive emissions of toxic gas in the Atlantic." *Nature* 415(6871): 493-494.
- Widdows, J., R. I. E. Newell, et al. (1989). "Effects of Hypoxia and Anoxia on Survival, Energy-Metabolism, and Feeding of Oyster Larvae (*Crassostrea-Virginica*, Gmelin)." *Biological Bulletin*
- Witte, U., N. Aberle, et al. (2003). "Rapid response of a deep-sea benthic community to POM enrichment: an in situ experimental study." *Marine Ecology-Progress Series* 251: 27-36.
- Wu, R. S. S., P. K. S. Lam, et al. (2002). "Tolerance to, and avoidance of, hypoxia by the penaeid shrimp (*Metapenaeus ensis*)." *Environmental Pollution* 118(3): 351-355.
- Yin, K. D., Z. F. Lin, et al. (2004). "Temporal and spatial distribution of dissolved oxygen in the Pearl River Estuary and adjacent coastal waters." *Continental Shelf Research* 24(16): 1935-1948.