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Marine invertebrates in hypoxia: Developmental, behavioural, physiological and fitness responses

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Abstract

Hypoxia is occurring in the marine environment all around the world as a result of human activities and natural biological processes such as eutrophication and water stratification. Low levels of dissolved oxygen (DO) can result in mass mortality and disruption for marine organisms. In this paper the effects of hypoxia ($<5\text{mg O}_2 \text{ l}^{-1}$) will be reviewed focusing on developmental, behavioural, physiological and fitness responses of marine invertebrates. Differences in the units used and thresholds when measuring hypoxia, by different researchers, make comparisons difficult. It is clear that negative effects are being observed at higher levels than the $2.8\text{mg O}_2 \text{ l}^{-1}$ threshold previously proposed by Diaz and Rosenberg. Many responses to hypoxia seem to not affect marine invertebrates directly, but result in a decrease in reproductive output and physiological mechanisms for surviving long-term hypoxia seem to be poorly understood. More research should be completed above the $2.8\text{mg O}_2 \text{ l}^{-1}$ threshold, and a priority should be quantifying the effects of hypoxia. Therefore, management targets can be enforced and a positive step can be made to combat hypoxia.

Key words: hypoxia; development, fitness, physiology, behaviour, invertebrate

Introduction

Normal dissolved oxygen levels in coastal waters range between 5.0 and 8.0mg O₂ l⁻¹ (Diaz & Rosenberg 1995). A low level of oxygen is termed hypoxia whereas a complete lack of oxygen is known as anoxia (Diaz 2001). Hypoxia is usually associated with semi-enclosed water bodies, which when combined with natural water-column stratification, restricts water exchange (Diaz et al. 2008). Since only organisms that can live without oxygen, e.g. microbes, live in these areas they are commonly called dead zones (Diaz & Rosenberg 2008). Diaz & Rosenberg (1995) suggested that waters become hypoxic when they reach a level of 2.8mg O₂ l⁻¹ or lower. This is the level at which mass mortality and large levels of disruption occur to benthic communities (Diaz & Rosenberg 1995). Recent studies are finding significant effects of low dissolved oxygen (DO) at levels higher than the threshold of 2.8mg O₂ l⁻¹ (Chan et al. 2008). Due to this, in this review hypoxia shall be considered as < 5mg O₂ l⁻¹ as this is when coastal waters stop having a normoxic level of DO. Hypoxia has been known to occur naturally in the marine environment, but can also arise as a result of human activities.

Hypoxia can arise naturally in large Enteromorpha-filled high shore rock pools overnight when photosynthesis is not occurring (McAllen 1998). In the open sea high levels of nutrients from upwelling can lead to high phytoplankton production, which leads to high levels of organic material. This material is decomposed by bacteria, which consume a lot of oxygen in the process. These hypoxic areas are called oxygen minimum zones and can result from a high demand for oxygen from elevated productivity and reduced circulation of already oxygen-poor water (Kamykoski & Zentara 1990). Naturally occurring hypoxia is becoming more frequent around the world as a consequence of global climate change (GCC). Changes in temperature, sea-level, hydrological processes and wind patterns eventually altering the world's currents could cause stronger stratification of water. Along with increased nutrient loading in coastal waters hypoxia could occur more frequently (Rabalais et al. 2009).

Most systems being studied for the impacts of hypoxia were not hypoxic when first studied. Since the middle of the last century it appears as though the increase in hypoxic areas coincides with an increase in human activities and eutrophication (Diaz et al. 2008). Eutrophication has been described as an increase in the rate of supply of organic matter into an ecosystem, usually occurring due to an imbalance in the nitrogen cycle (Nixon 1995, Howarth et al. 1996). High levels of oxygen are needed to decompose organic matter caused by high nutrient levels and places that were once normoxic become hypoxic (Gilbert et al. 2005, Cadée & Hageman 1974). Climate change, increased population, and more intense agriculture are intensifying the effects of eutrophication (Rabalais et al. 2009). Eutrophication was identified by the Group of Experts of Scientific Aspects of Marine Pollution (GESAMP) in 1990 as 'one of the major causes of immediate concern in the marine environment'. In the latest report (GESAMP 2008) combating eutrophication is still listed as a future challenge and priority in the marine environment. As hypoxia is an inevitable consequence of eutrophication, combating eutrophication could have profound effects for reducing hypoxic occurrences.

Hypoxia is occurring in thousands of kilometres of coastal areas around the world including the Adriatic Sea, Baltic Sea, Black Sea, Yellow Sea, Gulf of Thailand, Gulf of Mexico, Chesapeake Bay and the East China Sea (Rabalais & Turner 2001, Gray

et al. 2002, Chen et al. 2007). There has been an exponential growth rate of the occurrence of hypoxic events, at coastal sites, of 5.54% year⁻¹ (Vaquer-Sunyer & Duarte 2008). This apparent rapid increase in hypoxic events over time may not be as extreme as the data suggests. Recently there has been an increase in interest in hypoxia since it has become widely accepted to be a problem, which could have caused an increase in monitoring. Also, more recent developments could have led to an increased ability to detect and monitor hypoxia.

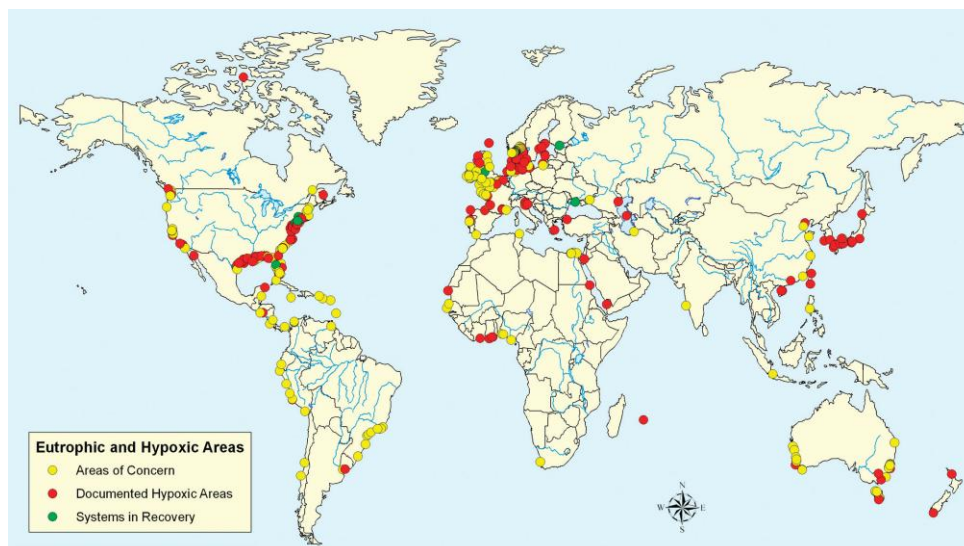


Figure 1: World hypoxic and eutrophic coastal areas. Data compiled from various sources by Diaz, Selman & Sugg (Selman et al. 2008)

Eutrophication-generated hypoxia is occurring in the Gulf of Mexico, Baltic Sea and Black Sea, with areas of hypoxia extending up to 20,000km², 84,000km² and <20,000km² respectively (Rabalais & Turner 2001, Mee 2001)(Figure 1). Hypoxia also occurs naturally on much larger scales at continental margin seafloors and oxygen minimum zones (Helly & Levin 2004). Tolo Harbour in Hong Kong has suffered from eutrophication and hypoxia for the past 20 years, which has caused mass mortalities of benthic organisms during summer water stratification (Wu 1982).

Low oxygen can affect organisms in a variety of ways including direct mortality, forced migration, an increased susceptibility to predation, changes in food resources and a disruption of life cycles (Diaz & Solow 1999). Hypoxia is also having an indirect effect on marine resources, such as fish catch. The northern Gulf of Mexico exhibits a correlation between the size of the hypoxic zone and the amount of shrimp caught (O'Connor & Whittall 2007). When levels of dissolved oxygen fall below critical levels, animals that are capable of escape, such as shrimp, move away from the area. Less mobile animals stay within the area of hypoxia and as a result can experience high stress and even mortality if levels fall low enough (Diaz & Rosenberg 1995). The aim of this article is to compile the work that has been completed on marine invertebrates exposed to hypoxia. A variety of effects of hypoxia on marine invertebrates and their responses will be discussed and reviewed below. Behavioural, developmental, physiological and fitness responses will be considered.

Behavioural responses

Behavioural responses to low oxygen have been observed during development and at full maturity. Embryos of *Acanthina monodon*, a marine gastropod, have been found to exhibit cannibalistic behaviour towards other embryos under increasing hypoxia. It is presumed that this is to reduce competition of already limiting oxygen (Lardies & Fernández 2002). At <25% oxygen water saturation *Nephrops norvegicus* leave their burrows and at <20% saturation they extend their legs so that they stand higher on the sediment and stop feeding (Baden et al. 1990). *N. norvegicus* has also been shown to cease digging behaviour at 2.5mg O₂ l⁻¹ (Eriksson & Baden 1997). This could be to reduce energy expenditure under low DO. At moderate and severe levels of hypoxia, 2.6 and 1.1mg O₂ l⁻¹ respectively, the bivalve *Macoma balthica* decreased its burial depth within 72 hours, increasing the risk from predators at the surface of the sediment (Long et al. 2008). *M. balthica* also expose their siphons out of the sediment into the water under hypoxia, which could ultimately lead to increased siphon nipping by predators (Seitz et al. 2003). Heavy mortality has been observed of *M. balthica* in the field under moderate hypoxia compared to the levels observed in this experiment. This suggests that there may be another factor that exacerbates the impacts of hypoxia *in situ* (Long et al. 2008).

Reduced feeding, as with *Nephrops norvegicus*, has been observed in adult *Nassarius festivus* and *Ruditapes decussates*, with the percentage of food being consumed decreasing with reduced DO (Cheung et al. 2008, Sobral & Widdows 1997). Siikavuopio et al. (2007) investigated the effect of hypoxia on the food consumption of the green sea urchin, *Strongylocentrotus droebachiensis*. It was found that total food consumption was significantly reduced in both of the hypoxic treatments, 4.0 and 6.0mg O₂ l⁻¹. It could be inferred that these marine invertebrates are reducing their food consumption as less energy is required due to the organism going into a hypometabolic state for survival. Reduced food and ultimately energy intake could have an indirect effect on reproductive output which will be considered in the next section.

Fitness responses

A reduction in energy allocation to reproduction was observed in *Nassarius festivus* with decreasing oxygen, signifying that the adults may be adapting a strategy to increase their survival rather than reproductive output (Cheung et al. 2008). Gonad growth in *Strongylocentrotus droebachiensis* was significantly reduced under hypoxic treatments, as well as reduced feeding (Siikavuopio et al. 2007). It was inferred that gonad growth was reduced due to impaired feeding in *S. droebachiensis*, but reduced reproductive output as a result of decreased feeding was not confirmed in *N. festivus*. Reduction in gonad growth could result in reduced Darwinian fitness due to a decrease in reproductive output.

Heterochrony, a phylogenetic difference in the timing of development, was observed in the brine shrimp, *Artemia franciscana* (Spicer & El-Gamal 1990). This heterochrony eventually resulted in a decrease in Darwinian fitness, with the hypoxia cultured brine shrimp having a significant decrease in lifetime reproductive output compared to the normoxic treatment (Spicer & El-Gamal 1990). As with *A. franciscana* the copepod, *Acartina tonsa*, produces significantly less eggs in hypoxic treatments, 1.5ml⁻¹ and 0.7ml⁻¹, and at 0.7ml⁻¹ survival of the eggs was significantly reduced compared to normoxia (Marcus et al. 2004).

It could be that as with *Nassarius festivus* and *Nephrops norvegicus*, hypoxia has an impact on the current generation, but the most significant implications may be exhibited in the future generations of the population. Copepods, such as *Acartina tonsa*, are important members of marine food webs and it may be that the timing of hypoxic events may play an important role in structuring, not only copepod populations, but also indirectly the community dynamics (Sedlacek & Marcus 2005). More recent work completed on *A. tonsa* has shown that hypoxia may have a greater affect in the summer months. At 15 and 25°C, hypoxia resulted in a lower egg production. At 15°C a decrease in egg production could be attributed to a decrease in body size rather than individuals producing fewer eggs, which was coincidentally observed in the 25°C treatment (Richmond et al. 2006). This study, along with Long et al. (2008), suggests that temperature and other environmental factors exacerbate the impacts of hypoxia.

Developmental responses

Recent work on *Nassarius festivus*, suggests that there are significant impacts of hypoxia at higher levels than the threshold of 2.8mg O₂ l⁻¹ suggested by Rosenberg & Diaz (1995). When DO was reduced to 3.0mg O₂ l⁻¹, embryonic development was significantly delayed and by further reducing the concentration to 0.5mg O₂ l⁻¹ no embryos successfully hatched (Chan et al. 2008). Longer developmental rates were also observed in the veliger larvae with metamorphosis being delayed at 4.5mg O₂ l⁻¹ and all larvae dying before metamorphosis could occur at 3.5mg O₂ l⁻¹. Veliger larvae were more sensitive than the embryos to low oxygen and more research may need to be completed on many different stages of development. Adult *N. festivus* exhibit reduced feeding under hypoxia so it could be that the veliger larvae also exhibit this behaviour, which could explain longer developmental times (Cheung et al. 2008). A longer development for pelagic larvae could increase their rate of predation suggesting that hypoxia can have indirect as well as direct effects on an organisms' survival.

As with *Nassarius festivus* veliger larvae, the copepod *Tigriopus brevicornis* does not reach crucial life stages when development occurs under hypoxia. At a DO of 1.0mg O₂ l⁻¹ *T. brevicornis* all died before reaching Copepodite stage 1 in development (M^cAllen & Brennan 2009). Hypoxia does not only affect developing embryos, but also development of juveniles. Juvenile *Crassostrea virginica*, kept within 1.5mg O₂ l⁻¹ have a 50% mortality rate by 131hours and within the first 144hours juveniles have grown only a third compared to the normoxic treatment (Baker & Mann 1992). Delayed development has also been observed in the oyster *Crassostrea virginica* and the mussel *Mytilus edulis* when kept in hypoxic conditions (0.6-1.3mg O₂ l⁻¹ for 60 hours), opisthobranch embryos when DO is reduced to 10% air saturation and the gastropod, *Chorus giganteus* at 50% air saturation (Widdows et al. 1989, Wang & Widdows 1991, Strathmann and Strathmann 1995, Cancino et al. 2003). At 50% air saturation, *C. giganteus* were also unable to hatch and developing embryos were observed to be lacking a shell, the hatchlings main defence. Shell secretion may have been inhibited due to a low intracapsular O₂ or low intracapsular pH, ultimately resulting in a divergence of carbonates away from shell calcification (Cancino et al. 2003).

Brine shrimp, *Artemia franciscana* have been found to be able to regulate their oxygen uptake under acute hypoxia from early stages in their development. Under

chronic hypoxia (10kPa) the brine shrimp were found to be able to regulate oxygen uptake earlier in their development (Spicer & El-Gamal 1990). A shift in *Artemia* oxygen affinity takes place at the same time as the gills and heart development, which has been suggested to be linked with an increase in haemoglobin (Spicer & El-Gamal 1990). As with most hypoxia-related studies, the responses are well documented but, more work needs to be completed to understand the underlying physiological mechanisms.

Physiological responses

Intracapsular oxygen availability is often a problem for organisms that undergo encapsulated development. Brante et al. (2009) have found that hypoxia (60% air saturation) affects the growth rate of *Crepidula fornicata* and *Crepidula coquimbensis*, both encapsulated gastropods, during development. Despite this, *C. fornicata* have been known to reach near anoxia conditions by the end of development *in situ*. It could be that the embryos have a physiological response to compensate for low oxygen conditions that are yet to be understood (Brante et al. 2009).

Nassarius festivus can reduce oxygen consumption rates significantly in low dissolved oxygen (Cheung et al. 2008). Similarly, *Ruditapes decussates*, *Callinectes sapidus* and *Eurypalopeus depressus* have been shown to depress their metabolic rates during hypoxia (Sobral & Widdows 1997, Stickle et al. 1989). At 25% air saturation *C. sapidus* and *E. depressus* decrease their metabolic rate by 32% and 47% respectively (Stickle et al. 1989). Growth was found to be always positive, in *R. decussates*, even though metabolism had been reduced and it was suggested that the clam can maintain aerobic catabolism under hypoxia (Sobral & Widdows 1997). It is possible that these individuals are decreasing their metabolism and undergoing a form of "hibernation". Under short-term hypoxia this strategy could benefit individuals by allowing them to survive, but if hypoxia persists reproductive output and growth could be considerably compromised. It could be inferred that hypoxia does not only act directly on individuals, but also on the long-term viability of a population.

Strongylocentrotus droebachiensis have been shown to have a low tolerance to hypoxia and no ability to be able to acclimate overtime. It was suggested that this could be due to a lack of respiratory pigment in the water vascular system (Siikavuopio et al. 2007). On the other hand, *Artemia* and *Daphnia* are able to increase haemoglobin under hypoxic stress, allowing them to survive longer periods in hypoxia (Bowen et al. 1969, Magnum 1990). The sea cucumber, *Holothuria forskali*, has been shown to be able to swell under low oxygen (60-70% water saturation) so that oxygen can diffuse more readily, but when faced with severe hypoxia (<15Torr) sea cucumbers eviscerate to reduce metabolic requirements (Astall & Jones 1991). Desai et al. (2009) found that nauplii of *Balanus amphitrite* are able to increase their enzymatic activity (catalase and superoxide dismutase) under low oxygen conditions, which proposes an antioxidant defence.

Conclusion

Work that has been completed on the responses of marine invertebrates to hypoxic conditions is very variable, with different parameters for measuring dissolved oxygen being used in different articles e.g. Torr, kPa, mg O₂ l⁻¹ and ml⁻¹. Different

parameters for measurement along with inconsistent thresholds for classifying hypoxia make comparisons between studies difficult. The threshold for classifying hypoxia proposed by Rosenberg & Diaz (2005) of $2.8\text{mg O}_2\text{ l}^{-1}$ seems to be used by some, but many effects are being seen at higher levels of dissolved oxygen, e.g. *Nassarius festivus* which has delayed development at $4.5\text{mg O}_2\text{ l}^{-1}$ (Chan et al. 2008). Coincidentally, earlier development was observed in *Artemia franciscana* when exposed to hypoxia (10kPa) (Spicer & El-Gamal 1990). As organisms respond differently to hypoxia, imposing a threshold level of hypoxia for all marine invertebrates may cause researchers to overlook important responses. It could be suggested that research should be completed on marine invertebrates at any level below normoxic conditions of $5\text{mg O}_2\text{ l}^{-1}$.

Not only is variation in tolerance observed within the marine invertebrates, but also between families. Molluscs have been regarded as being the most tolerant of marine invertebrates to low dissolved oxygen, having an average LC_{50} (lethal concentration) of $1.99 \pm 0.16\text{mg l}^{-1}$ (Vaquer-Sunyer & Duarte 2008). The gastropods, *Thais haemastoma* and *Stramonita haemastoma*, have been known to have a high tolerance to hypoxia, LC_{50} $0.79\text{mg O}_2\text{ l}^{-1}$ and $0.51\text{mg O}_2\text{ l}^{-1}$ respectively (Kapper & Stickle 1987, Das & Stickle 1993). An exception to this seems to be the green abalone, *Haliotis laevis*, with an LC_{50} of $5.91\text{mg O}_2\text{ l}^{-1}$, suggesting that there may be more variation within phyla than is realised (Harris et al. 1999). More research needs to be conducted to understand how different organisms within a family react to hypoxia and using average family LC_{50} values should be avoided.

Different effects of hypoxia are observed between veliger larvae and embryos of the gastropod *Nassarius festivus* (Cheung et al. 2008). It could be that many marine invertebrates exhibit altered abilities of response during different life stages and this should be further investigated. Spicer and El-Gamal (1990) found an accelerated development in *Artemia franciscana*, seemingly beneficial to the brine shrimp, but reproductive output was significantly decreased in the hypoxic treatment. Without the authors' progression of this study, no negative response to hypoxia would have been observed. Organisms should be studied in depth so that all aspects of life history are assessed when hypoxia is involved.

The question arises as to how accurately the laboratory experiments resemble what is occurring *in situ*. *Macoma balthica* in the lab requires severe hypoxia to cause mortality, compared to moderate levels *in situ* (Long et al. 2008). Also, *Crepidula fornicata* can reach anoxic conditions during development in the field, but was found to have a decrease in growth rate in the lab under hypoxia (Brante et al. 2009). These studies suggest that observations under lab conditions may not accurately resemble the impacts of hypoxia. GCC could have profound effects on the marine environment and ultimately unpredictable effects on areas of hypoxia, by altering other conditions such as temperature and salinity (Rabalais et al. 2009). More work needs to be completed to determine how low DO interacts with other environmental conditions such as temperature and salinity, ultimately helping to explain some of the variation observed between the lab and field.

Significant progress has been made in identifying hypoxic occurrences and in recognising the effects and responses of marine invertebrates subjected to hypoxia. Despite this, physiological mechanisms for surviving hypoxia seem to be poorly

understood, with a need for long-term experiments. With these, it can be determined as to whether physiological mechanisms can change over generations so that organisms that once couldn't survive within low oxygen ultimately evolve to be able to.

Most hypoxic studies seem to focus on the individual and little is known about the effects on higher trophic levels and community dynamics. As eutrophication appears to be responsible for the increase in hypoxia over the last century, implementation of nutrient management plans needs to be completed in areas of severe hypoxia (Diaz et al. 2008). This is costly and more research needs to be completed to identify the full magnitude of the effect of hypoxia on the marine community prior to this. Indirect effects of hypoxia on higher trophic levels and the quantification of the impacts of hypoxia need to be a priority in the field, so that management targets can be imposed and a positive step can be made in combating hypoxia.

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