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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)	

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Non-technical summary

Hypoxia is a mounting problem affecting the world's coastal waters, with severe consequences for marine life, including death and catastrophic changes. The deleterious effects of hypoxia can be amplified by warming. Global warming will contribute to decrease the global average dissolved oxygen in the oceans worldwide, and may also affect the oxygen requirements of marine benthic macrofauna. Increasing temperature diminishes oxygen solubility and increases the respiration rates of organisms, as temperature plays a fundamental role in regulating metabolic processes. Increased temperature will likely affect the responses of marine benthic organisms to hypoxia because metabolic rates increase exponentially with temperature. Ocean warming is expected to increase the vulnerability of benthic macrofauna to reduced oxygen concentrations and expand the area of coastal ecosystems affected by hypoxia. Here we evaluate the effects of warming in the oxygen thresholds for benthic macrofauna with the basis of a literature survey.

Introduction

Oxygen deficiencies have increased in frequency, duration and severity in the world's coastal areas during the last decades (Diaz and Rosenberg, 2008).

Hypoxia decreases abundance and diversity of the benthic macrofauna (e.g. Josefson and Widbom, 1988; Diaz and Rosenberg, 1995). Changes in the benthic macrofauna community observed after episodes of severe oxygen deficiency have been correlated to differential tolerance to low oxygen concentrations (Diaz and Rosenberg, 1995; Vaquer-Sunyer and Duarte, 2008).

These tolerances vary significantly between taxonomic groups. In general, molluscs and polychaetes are more tolerant to low oxygen than echinoderms, fishes and crustaceans (Vaquer-Sunyer and Duarte 2008). Oxygen tolerances are modulated by environmental factors such as the presence of hydrogen sulphide (Vaquer-Sunyer and Duarte, 2010) or hypercapnia (elevated $p\text{CO}_2$) and low pH (Boleza *et al.*, 2001; Rosa and Seibel, 2008). Warming may also contribute to exacerbate hypoxia and its consequences for marine life.

Global warming is forecasted to lead to increase the mean global temperature by 1.8 to 4 °C by the end of the 21st Century (Meehl *et al.*, 2007), with important consequences on climate, hydrology, biodiversity, and biogeochemical cycles. Impacts from global warming will combine with those derived from other human pressures, such as the impacts derived from excess nutrient inputs, which is a major driver of the proliferation of hypoxia in the coastal ocean (Cloern, 2001; Kemp *et al.*, 2009).

Temperature is a key factor controlling the extent of hypoxia (Conley *et al.*, 2007; Conley *et al.*, 2009), acting through a multitude of interacting processes, including temperature effects on increasing stratification and reducing ventilation of marine waters (Sarmiento *et al.*, 1998). The possibility of strengthened stratification alone, from increased surface water temperature, is enough to worsen hypoxia where it presently exists and will trigger its occurrence in other coastal areas (Rabalais *et al.*, 2009).

Increasing temperature diminishes oxygen solubility (Carpenter, 1966; Garcia and Gordon, 1992), and increases the respiration rates of organisms (Jones, 1977; Enquist *et al.*, 2003), as temperature plays a fundamental role in regulating metabolic processes (Iriberry *et al.*, 1985; White *et al.*, 1991).

Increased temperature will likely affect the responses of marine benthic organisms to hypoxia because metabolic rates increase exponentially with temperature (Brown *et al.*, 2004). Whereas both photosynthesis and respiration are enhanced with warming, Metabolic Theory of Ecology (MTE, Brown *et al.*, 2004) predicts that respiration rates should increase faster with warming than photosynthetic rates as activation energies for autotrophic processes are half of those for heterotrophic processes (Harris *et al.*, 2006). However, increased temperature may also affect the vulnerability of organisms to low oxygen concentration, as the increased organismal

respiration rates increases their oxygen demand, affecting the oxygen thresholds for hypoxia. Here we evaluate, on the basis of a meta-analysis of available experimental results, the effects of temperature on the oxygen thresholds for marine benthic macrofauna.

Methods

A broad Literature search (Web of Science and Scholar Google) was used to assess the effects of temperature in modulating the thresholds of hypoxia for marine benthic communities.

Compiling the negative effects of hypoxia and the effects of temperature in modulating these effects 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 oxygen concentration. The toxicity tests for which a broader empirical basis was found in the literature are:

-Median lethal concentration (LC50): Statistically derived concentration of a substance in an environmental medium expected to kill 50% of organisms in a given population under a defined set of conditions*.

-Median sublethal concentration: (SLC50): Statistically derived concentration of a substance in an environmental medium expected to produce a negative effect on the 50% of organisms in a given population under a defined set of conditions*.

-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)

Quantile regression was used to assess changes in the probability distribution of thresholds of hypoxia for marine benthic organisms with increasing temperature. The response of the thresholds of hypoxia, as described by LC₅₀ (% sat. and mg O₂ L⁻¹) and LT₅₀ (h), to temperature was described by fitting the relationship between the 95%, 50% (median) and 5% quantiles for the distribution of these thresholds and water temperature. Quantile regression estimates multiple rates of change (slopes), from the minimum to maximum response, providing a more complete description of the relationships between variables missed by other regression methods focused on prediction of the mean value (Cade & Noon 2003). Quantile regression can be considered as an extension of classical least squares estimation of conditional mean models to the estimation of a compilation of models for several conditional quantile functions, considering the median as the central parameter (Koenker 2005). Statistical analyses were performed using JMP 7.02 for simple regression analyses, ANOVA and ANCOVA, and R for quantile regression.

The Q_{10} (the relative rate of increase in a given rate expected for a 10°C temperature increase) was calculated by fitting, using least squares linear regression, the equation (Raven and Geider, 1988):

$$Q_{10} = e^{\left(\frac{10E_a}{RT^2}\right)}$$

, where R is the gas constant (8.314472 mol⁻¹ K⁻¹), T is the mean absolute temperature across the range over which Q_{10} was measured (K), and E_a is the activation energy (J mol⁻¹), derived from the slope of the Arrhenius equation relating the natural logarithm of the given rate to 1/kT, where k is the Boltzmann's constant (8.62 × 10⁻⁵ eV k⁻¹) and T is the temperature (Kelvin). The slope of this relationship is the activation energy (E_a) in eV, which can be converted to J mol⁻¹ using a conversion factor of 96486.9.

Results

We found a total of 363 published experiments involving 108 species pertaining to 10 different taxonomic groups of benthic macrofauna reporting the water temperature at which the median lethal time (LT₅₀, h) was assessed (Fig. 1a) and 213 experimental assessments involving 39 species from 3 different taxonomic groups (mollusca, fishes and crustaceans) of benthic marine fauna reporting the incubation temperature at which the median lethal concentration (LC₅₀, % saturation and mg O₂ L⁻¹) was assessed (Fig 1b,c).

Examination of the relationship between LT₅₀ and experimental temperature showed that the range of LT₅₀ values observed declined with increasing temperature, with most experiments conducted showing relatively low LT₅₀ values at high temperature (Fig. 1a). This was confirmed using quantile regression fitted to the 95% and the 5% quantiles as well as the 50% quartile (median) of the change in LT₅₀ with increasing temperature (Fig 1a). The 95% quantile regression, estimating the temperature dependence of the maximum LT₅₀ expected for a given water temperature, indicated a decrease in the maximum LT₅₀ by 63.62 ± 19.10 hours per each degree of temperature increase, whereas the 5% quantile regression, estimating the temperature dependence of the minimum LT₅₀, showed only a decrease by 0.45 ± 0.31 hours (27 minutes) for each degree Celsius increase. The median LT₅₀ declined by 3.95 ± 1.67 hours for each degree Celsius of temperature increase (Fig 1a). The variability in LT₅₀, as described by the 5% to 95% interquantile range, declined with increasing temperature from values of 12.95 to 1956.25 hours at the lower end of marine temperature (0 °C) to 0 to 47.5 hours at the high end (30 °C, Fig. 1a).

The intercepts and slopes of the regressions between LT₅₀ and experimental temperature showed significant differences among taxonomic groups. No significant relationship between LT₅₀ and temperature was found for fish, crustaceans, annelids, cnidarians, bryozoans, echinoderms and platyhelminthes, but Priapulidans showed the steepest decline in median lethal time (205.2 ± 2.08 hours ° C⁻¹, R² = 0.99, p < 0.007, N = 3), whereas molluscs showed a much smaller decrease in survival time (41.90 ± 5.46 hours ° C⁻¹, R² = 0.25, p < 0.0001, N = 189) with warming.

The relationship between LC₅₀ (% sat.) and experimental temperature showed increasing

variability in LC_{50} and increasing median lethal oxygen concentrations with increasing temperature. Quantile regression describing the relationship between the 95% quantile of LC_{50} and water temperature showed an increase in LC_{50} (% sat.) by 2.75 (± 0.47) % saturation (i.e. 0.15 (± 0.04) $\text{mg O}_2 \text{ L}^{-1}$) per each degree Celsius increase, whereas the 5% quantile regression increased by only 0.50 (± 0.15) % saturation (i.e. 0.03 (± 0.01) $\text{mg O}_2 \text{ L}^{-1}$) for each degree Celsius of temperature increase. The median LC_{50} (% sat.) increased by 1.02 (± 0.15) % saturation (i.e. 0.03 (± 0.01) $\text{mg O}_2 \text{ L}^{-1}$) for each Celsius degree of temperature increase (Fig 1b,c). The variability in LC_{50} (% sat.), as described by the 5% to 95% interquartile range, increased with increasing temperature from 0.00 to 15.50 % saturation (i.e. 0.00 to 2.24 $\text{mg O}_2 \text{ L}^{-1}$) at the lower end of marine temperature (0 °C) to 11.63 to 98.00 % oxygen saturation (0.80 to 6.74 $\text{mg O}_2 \text{ L}^{-1}$) at the high end (30 °C, Fig.1b,c).

There were significant differences in the intercept and the slope of the relationships describing the temperature-dependence of LC_{50} (% sat.) for different taxonomic groups, as no significant relationship between LC_{50} (% sat.) and temperature was found for fish, which may be a consequences of the range of physiological capacities in the fish species included in the data set. Crustaceans showed the highest increase in median lethal O_2 concentration with warming (2.40 ± 0.36 % oxygen saturation $^{\circ}\text{C}^{-1}$, $R^2 = 0.26$, $p < 0.0001$, $N = 125$; i.e. 0.15 ± 0.03 $\text{mg O}_2 \text{ L}^{-1}$, $R^2 = 0.21$, $p < 0.0001$, $N = 124$) and molluscs showed the lowest increase in LC_{50} with warming (1.42 ± 0.36 % oxygen saturation $^{\circ}\text{C}^{-1}$, $R^2 = 0.40$, $p < 0.0007$, $N = 26$; i.e. 0.09 ± 0.02 $\text{mg O}_2 \text{ L}^{-1}$, $R^2 = 0.37$, $p < 0.001$, $N = 26$).

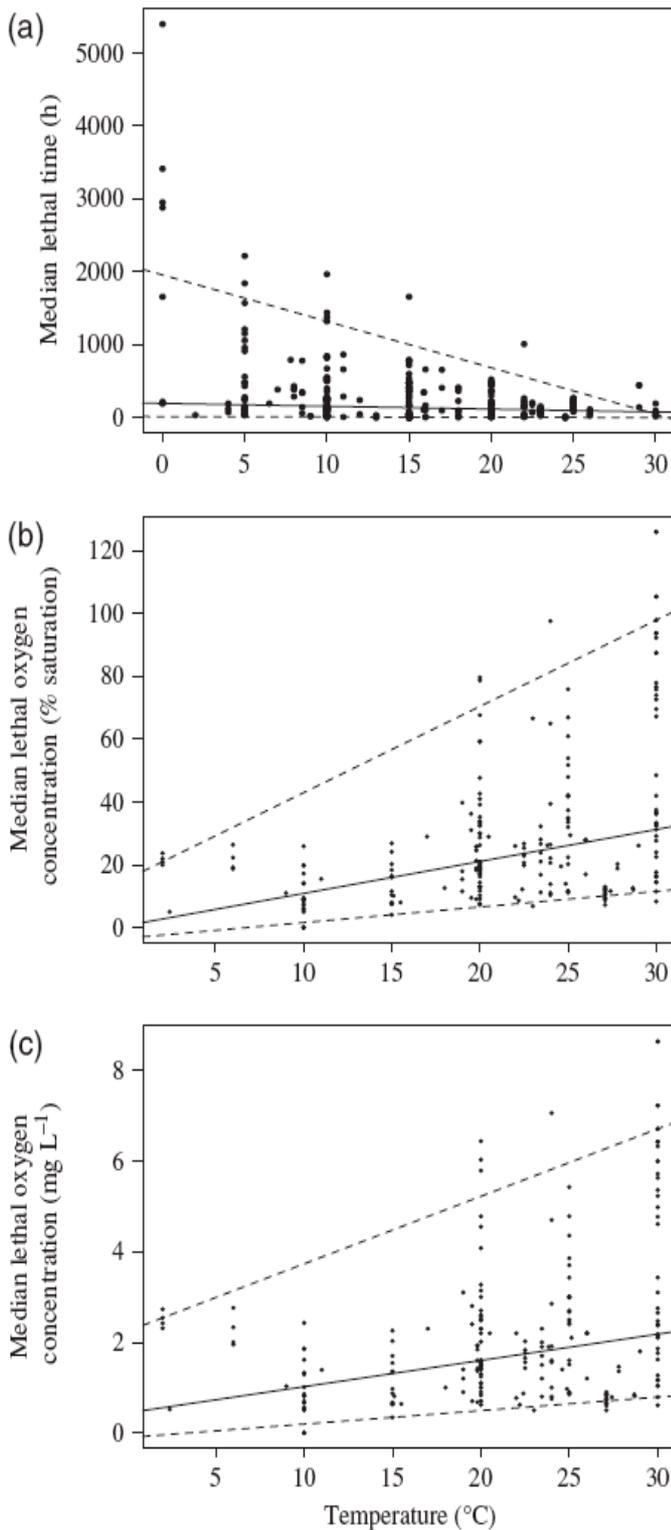


Figure 1. (a) The relationship between the median lethal time (LT₅₀, h) and water temperature for the different experiments. The solid line represents the fitted regression for the median or the 50% quartile [LT₅₀ (h) = 194.70 (±34.04) - 3.95 (±1.67) * temperature; N=363, P<0.03]. The dashed lines represent the fitted regression for the 95% quartile [LT₅₀ (h)=1956.25 (±430.54) - 63.62 (±19.10) * temperature; N =363, P<0.001] and the 5% quartile [LT₅₀ (h)=12.95 (± 6.63)-0.45 (± 0.31)*temperature; N=363, P=0.15]. (b) The relationship between the median lethal concentration (LC₅₀, %sat.) and the water temperature for the different experiments. The solid line represents the fitted regression for the median or the 50% quartile [LC₅₀ (%sat.) = 0.71 (±2.91) + 1.02 (±0.15)* temperature; N=213, P<0.0001]. The dashed lines represent the fitted regression for the 95% quartile (LC₅₀ (% sat.)=15.50 (±8.99)+2.75 (±0.47)*temperature; N=213, P<0.0001) and the 5% quartile (LC₅₀ (% sat.)=-3.37 (±3.62)+0.50 (±0.15)* temperature; N=213, P<0.002). (c) The relationship between the median lethal concentration (LC₅₀, mgO₂ L⁻¹) and the water temperature for the different experiments. The solid line represents the fitted regression for the median or the 50% quartile [LC₅₀ (mgO₂ L⁻¹)50.44 (±0.27)+0.06 (±0.01)* temperature; N=212, P<0.0001]. The dashed lines represent the fitted regression for the upper 95% quartile [LC₅₀ (mgO₂L⁻¹)52.24 (±0.68)+0.15 (±0.04)*temperature; n=212, P<0.0001] and the lower 5% quartile [LC₅₀ (mgO₂L⁻¹)=-0.10 (±0.32) +0.03 (±0.01)*temperature; N=212, P<0.02

We found a total of 189 published experiments involving 21 species from 5 different taxonomic groups of benthic macrofauna where the median lethal time (LT₅₀, h) of the subject organism was assessed at different temperatures and a total of 165 published experiments involving 10 species belonging to 3 different taxonomic groups (fishes, crustaceans and

molluscs) of benthic macrofauna where the median lethal oxygen concentration (LC_{50}) of the subject organism was assessed at different temperatures.

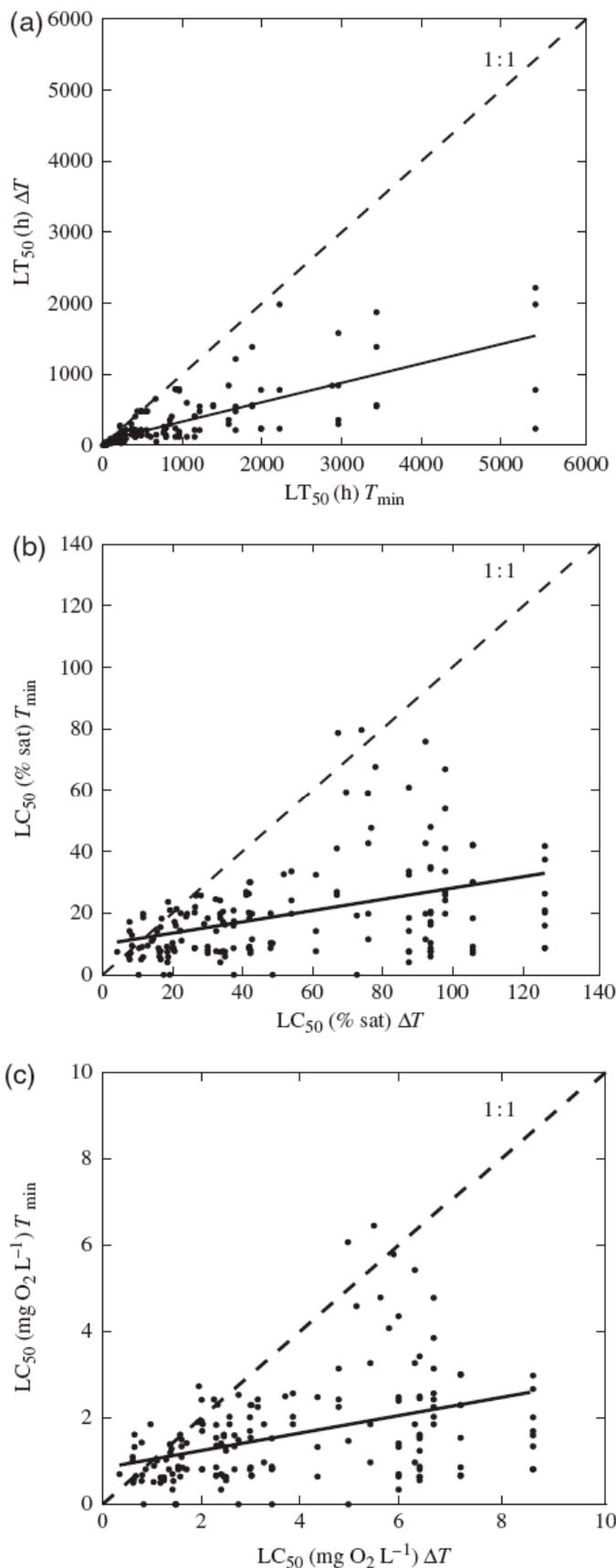


Figure 2. (a) The relationship between the median lethal time at increased temperature ($LT_{50} \Delta T$) and median lethal time at lower temperature (LT_{50}) (units: h). $LT_{50} \Delta T$ (h) = $80.04 (\pm 22.68) + 0.26 (\pm 0.02) * LT_{50}$ (h). ($R^2=0.54$, $P<0.0001$) $n=5189$. The solid line represents regression line and dashed line represents the line 1:1. (b) The relationship between the median lethal concentration at one temperature ($LC_{50} T_{min}$) and median lethal concentration at increased temperature ($LC_{50} \Delta T$) (units: % oxygen saturation). $LC_{50} T_{min}$ (% oxygen saturation) = $9.85 (\pm 2.01) + 0.18 (\pm 0.03) * LC_{50} \Delta T$ (% sat.). ($R^2=0.17$, $P<0.0001$) $N=165$. The solid line represents regression line and dashed line represents the line 1:1. (c) The relationship between the median lethal concentration at one temperature ($LC_{50} T_{min}$) and median lethal concentration at increased temperature ($LC_{50} \Delta T$) (units: $mg O_2 L^{-1}$). $LC_{50} T_{min}$ ($mg O_2 L^{-1}$) = $0.84 (\pm 0.16) + 0.20 (\pm 0.04) * LC_{50} \Delta T$ ($mg O_2 L^{-1}$). ($R^2=0.16$, $P<0.0001$) $N=165$. The solid line represents regression line and dashed line represents the line 1:1.

There was a strongly significant trend for the median lethal time under hypoxia to decrease as temperature increases (95.1% of the experiments), and only 2.9 % of the experiments reported LT_{50} to be unaffected by increasing water temperature (Fig. 2a, Wilcoxon ranked sign test, $p < 0.0001$). The median lethal time under hypoxic conditions was reduced by, on average (\pm SE), 74 ± 2 % when temperature was increased (Fig. 2a). There was a significant relationship between the ratio of LT_{50} (h) values at the minimum and maximum temperature tested ($\frac{LT_{50T_{\min}}}{LT_{50T_{\max}}}$) and the temperature increase (ΔT , ° C), as described by the fitted regression equation:

$$\frac{LT_{50T_{\min}}}{LT_{50T_{\max}}} = 0.81 + 0.21 (\pm 0.03) \Delta T (\text{°C}) \quad (R^2 = 0.19, p < 0.0001)$$

Calculated Q_{10} values for the change in LT_{50} (h) with increasing temperature showed a broad range of values with an average (\pm SE) Q_{10} describing the temperature-dependence of LT_{50} of 3.01 ± 0.29 (Fig. 3a). Analysis of covariance (ANCOVA) did not yield evidence of significant differences among taxonomic groups or life stages in slope or intercept (t -test, $p > 0.05$) in Q_{10} values for the change in LT_{50} with increasing temperature. Calculated Q_{10} values for the change in LT_{50} (h) with increasing temperature showed statistically significant differences among organisms with different motility capacities, with sessile organisms having higher Q_{10} values than organism with mobility ($F = 5.35$, $p < 0.02$).

There was a strongly significant trend for the median lethal oxygen concentration to increase with increasing temperature (93.3 % of the experiments, Wilcoxon ranked sign pair test, $p < 0.0001$, Fig. 2b). The median lethal oxygen concentration under hypoxic conditions increased by, on average (\pm SE), 81.7 ± 3.1 % and 79.9 ± 4 % when temperature was elevated in terms of % saturation (Fig. 2b) and concentration ($\text{mg O}_2 \text{ L}^{-1}$, Fig. 2c), respectively. Calculated Q_{10} values for the change in LC_{50} with increasing temperature showed an average (\pm SE) Q_{10} describing the temperature-dependence of LC_{50} of 2.08 ± 0.20 (in % sat., Fig. 3b) and of LC_{50} 1.80 ± 0.17 (in $\text{mg O}_2 \text{ L}^{-1}$, Fig. 3c). Analysis of variance (ANOVA) did not yield evidence of significant differences for taxonomic groups ($p > 0.05$). There were statistically significant differences for life stages, with larvae tending to have higher Q_{10} values for the change in LC_{50} (% sat) with increasing temperature than juveniles, but not than adults ($F = 3.43$, $p < 0.05$). Sessile organisms tended to have higher Q_{10} values for the change in LC_{50} (% sat) with increasing temperature than high mobile organisms or active swimmers, but not than organisms with reduced mobility ($F = 5.16$, $p < 0.006$).

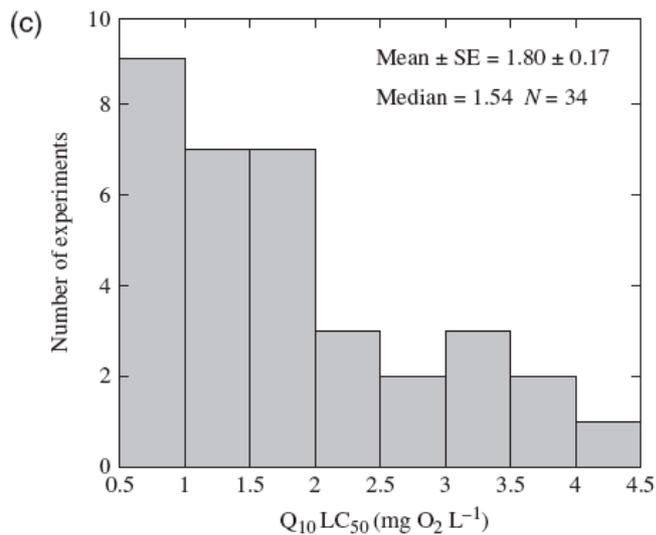
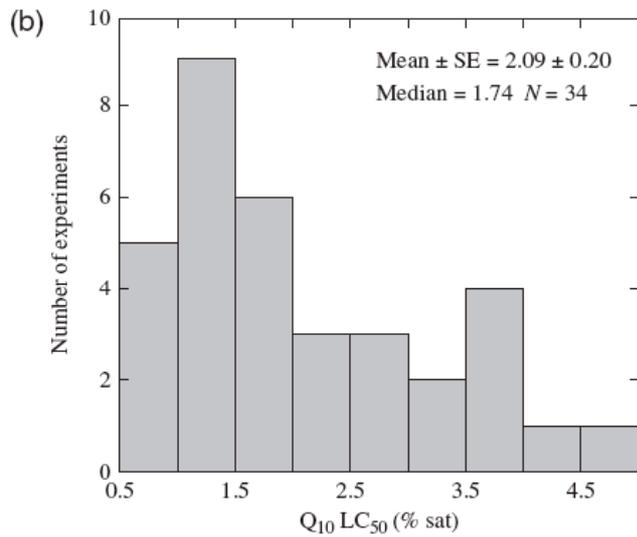
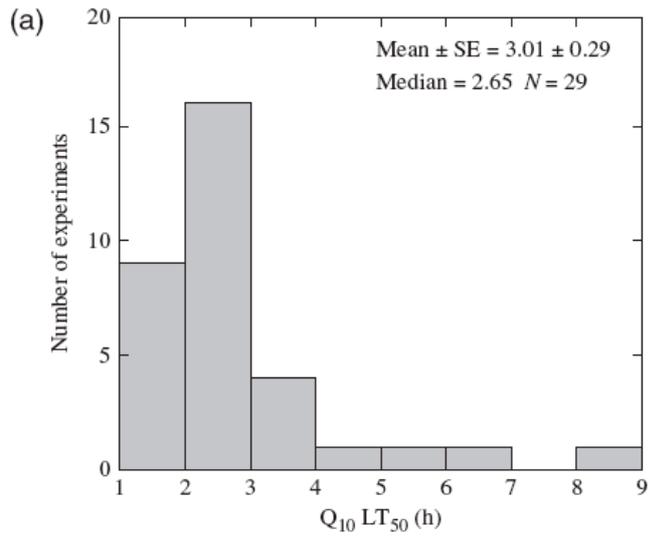


Figure 3. Frequency distribution for Q_{10} values for median lethal time (a) and for median lethal oxygen concentration in % sat. (b) and in mg O₂ L⁻¹ (c). Data on Q_{10} for median lethal time calculated from (Gamble, 1970; Dries and Theede, 1974; Shumway *et al.*, 1983; Oeschger and Theede, 1986; Stickle *et al.*, 1989; Brooks *et al.*, 1991; Johnson and McMahon, 1998; de Zwaan *et al.*, 2001) and on Q_{10} for median lethal oxygen concentration calculated from (Shimps and Rice, ; Vargo and Sastry, 1977; Stickle *et al.*, 1989; Schurmann and Steffensen, 1992; Hoback and Barnhart, 1996; Plante *et al.*, 1998; Miller *et al.*, 2002; Cerezo and Garcia, 2004; Ishibashi *et al.*, 2005; Shimps *et al.*, 2005; Goodman and Campbell, 2007).

Discussion

The results presented support the hypothesis that the thresholds of hypoxia for benthic marine macrofauna are significantly affected by temperature and provide estimates of the extent of change in thresholds of hypoxia with increasing temperature. However, is derived for a data set including a limited set of species, so that the generality of the conclusions reached here must be tested further when data for species not included here become available. Moreover, these results derive from experiments where temperature changes were imposed over short time scales, whereas microevolutionary changes may increase the resistance of organisms to hypoxia as the oceans warm along the 21st Century, so that the predictions resulting from this analysis may provide worst-case scenarios that can be refined with data derived from documented responses of benthic communities to hypoxia in the future.

The results from this meta-analysis indicates that the survival time of benthic organisms under hypoxia is reduced and the oxygen concentration at which high mortality (LC₅₀, % sat.) takes place increases with increasing temperature, indicating that the oxygen requirements of benthic macrofauna increase with increasing temperature. Moreover, the range of survival time and the median lethal oxygen concentration for benthic macrofauna are also significantly affected by increasing temperature.

Examination of the relationship between LC₅₀ (% sat.) and water temperature showed that the range of median lethal O₂ concentration increased significantly with increasing water temperature, suggesting that the relationship between LC₅₀ (% sat.) and water temperature is complex, probably driven by differences on the effect of temperature on metabolism, possible differences between the experimental temperature and the temperature within the ecosystem where the organisms were living, taxonomic differences in the sensitivity to hypoxia and warming, different life stages, and different species-specific physiological limitations, among others. Crustaceans, the group most vulnerable to hypoxia, were the organisms with the highest oxygen requirements for survival at any one temperature, showing an increase in the median lethal O₂ concentration of 0.24 mg O₂ L⁻¹ per each degree Celsius of warming, and an even steeper increase for the 95% quantile (0.31 ± 0.06 mg O₂ L⁻¹ °C⁻¹). This confirms earlier indications that crustaceans are the most sensitive group to hypoxia (Vaquer-Sunyer and Duarte 2008), and shows that they are also the organisms with thresholds of hypoxia most sensitive to temperature.

Whereas the LT₅₀ (h) and LC₅₀ (% sat.) for individual species varies considerably for any water temperature, experimental temperature manipulations show an overwhelming tendency for individual species to the survival times under hypoxia and the oxygen requirements for survival to decrease and increase, respectively, with increasing temperature. The mean Q₁₀ values describing the temperature-dependence of the thresholds of hypoxia for benthic macrofauna are comparable to those describing the temperature dependence of respiration rates (Q₁₀ values around 2 - 3, cf. Neori and Holm-Hansen, 1982; Raven and Geider 1988), providing

evidence that the temperature-dependence of thresholds of hypoxia for benthic macrofauna is associated with increased metabolic oxygen demands at increasing temperature.

Q_{10} values either for median lethal time or median lethal oxygen content showed higher values for sessile species than for species with a higher degree of mobility. The implication of a high Q_{10} value for LC_{50} (%sat.) or LT_{50} (h) is that the oxygen requirements of sessile organisms will increase more with warming than for mobile organisms with the handicap that sessile organisms cannot escape the hypoxic area. The mean Q_{10} values for LT_{50} (h) for sessile species is 5.06, resulting in a decrease of their survival time by 25.3% and 47.7% with 1.8 °C and 4 °C warming, respectively. For an oyster (*Crassostrea virginica*) living in waters with 30 psu and 20°C, this reduction means a decrease in its survival time from 20 to 10 days with a 4°C warming and to 14 days with a 1.8°C warming. Reductions in survival time to half can lead to a significant reduction of the oyster population in areas such as Chesapeake Bay, where persistent seasonal hypoxia occurs and temperature is one of the key controls of hypoxia development (Kemp et al., 2009). The average Q_{10} values for LC_{50} (% sat.) for sessile species is of 3.72, resulting in an increase of median lethal oxygen content by 21.1 % and 40.9 % with warming of 1.8 °C, and 4 °C, respectively. The consequences for an oyster living at 20°C and 30 psu would be an increase of the oxygen requirements to survive, enhancing its LC_{50} (% sat.) from 19 % saturation (i.e. 1.46 mg O₂ l⁻¹) to 27 % or 23 % saturation (i.e. 1.95 or 1.71 mg O₂ l⁻¹) with warming of 4 or 1.8°C respectively.

The results reported here imply the existence of synergistic effects of hypoxia and warming greatly increasing the vulnerability of marine biota to hypoxia in a warmer ocean. Assessment of the impact of warming across the range from 1 to 6 °C expected across regions along the 21st Century on the survival time and the threshold oxygen concentrations for mortality of benthic macrofauna using the average Q_{10} values reported here predict that survival times will decrease by a mean of 10.4 to 48.4 % and the threshold oxygen concentrations for high mortality to occur will increase by, on average, between 7.1 to 35.7 % with increasing warming. Hence, ocean warming is expected to increase the thresholds of hypoxia-driven mortality of benthic macrofauna.

Oxygen concentrations are also expected to be reduced in a warmer ocean rendering the effects of ocean warming on hypoxia-driven mortality steeper than expected from the effect of temperature on the oxygen requirements of organisms shown here alone. In a recent paper, Conley *et al.* (2009) calculated that the hypoxic area in Danish coastal waters will double with a 4°C increase as a consequence of changes in oxygen solubility alone, maintaining all other factors unchanged. At the global scale, ocean models predict declines in global average dissolved oxygen, due to ocean warming, over the next century ranging between 1% and 7% (Keeling *et al.*, 2010). (Shaffer *et al.*, 2009) predicted long-term ocean oxygen depletion and a great expansion of ocean oxygen-minimum zones for scenarios involving high emissions or high climate sensitivity to green house emissions. Whereas Keeling et al. (2010) provide evidence for a global oxygen decline in ocean waters, rates of oxygen decline tend to be greater in coastal waters compared to open ocean ones (Gilbert *et al.*, 2010), consistent with observations around the world (Gilbert *et al.*, 2005; Bograd *et al.*, 2008; Diaz and Rosenberg, 2008). Yet, reduced

oxygen concentration with increasing temperature and increased oxygen requirements by benthic macrofauna are only two of a variety of processes affecting hypoxia in a warmer ocean, as a warmer ocean is also likely to show increased stratification, reducing ventilation, and an increased oxygen drawdown by respiratory processes, which are enhanced with increasing temperature (Brown et al., 2004; Harris et al., 2006).

Hence, ocean warming will produce an increase in the extent and severity of marine macrofauna mortality under hypoxia by the combined effect of reducing dissolved oxygen concentration in the ocean and increasing the oxygen requirements of organisms (Najjar *et al.*, 2010) and their sensitivity to reduced oxygen concentrations. The combined effect will produce further reduction in the quality and spatial extent of suitable habitat for a wide range of aerobic organisms. For example, Niklitschek and Secor, 2005) demonstrated, in a simulation on the combined effects of warming and hypoxia in the Chesapeake Bay system, that a small warming of 1 °C during summer months could practically eliminate suitable habitats for juvenile Atlantic sturgeon (*Acipenser oxyrinchus*). Indeed, the reduction of suitable habitat for fishery species could result in important losses for the fishery industry (Breitburg, 2002). Suitable habitat for most metazoans is restricted by water temperature, among other multiple factors, as all organisms live within a limited range of water temperatures, allowing optimized structural and kinetic coordination of cellular, molecular, and systemic processes (Portner and Farrell, 2008). Warming above the thermal window of the organisms can also trigger anaerobic metabolism (Portner and Farrell 2008).

The meta-analysis conducted here suggests that warming will negatively impact the survival of benthic organisms under low oxygen conditions by reducing survival times under hypoxia by a median of 3.95 ± 1.67 hours °C⁻¹ and by increasing the oxygen thresholds for hypoxia-driven mortality by a median of 1.02 ± 0.15 % saturation °C⁻¹ (0.07 ± 0.01 mg O₂ L⁻¹ °C⁻¹) across the species for which evidence is available. Hypoxia is already expanding globally across coastal waters (Diaz and Rosenberg, 2008; Rabalais et al., 2009; Rabalais *et al.*, 2010), parallel to increased flux of nutrients to the coastal zone and concurrent with a tendency for warming of coastal waters (Rabalais *et al.* 2009; Rabalais *et al.* 2010). The synergies between two global changes, oxygen depletion and warming the world's coastal waters, threaten benthic macrofauna in coastal ecosystems. Aggravation of the negative effects of spreading hypoxia by warming and the fact that warming will contribute to oxygen depletion in ocean waters suggest that the threats to marine biodiversity derived from hypoxia will be greater than anticipated.

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