Temperature effects on thresholds of hypoxia for marine benthic organisms.

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Abstract

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. The effect of warming on the oxygen requirements and the survival of benthic organisms under hypoxia was tested using a meta-analysis of published experimental results evaluating the effects of increasing temperature on the median lethal time and median lethal concentration of benthic macrofauna under hypoxia. The meta-analysis confirmed that survival times under hypoxia are reduced by an average of 74% and that median lethal concentration increases by a mean of 16% in marine benthic organisms exposed to higher temperatures. Warming reduced survival times of marine benthic macrofauna under hypoxia by a median of 3.95 ± 1.67 hours $ºC^{-1}$ and increased the oxygen thresholds for hypoxia-driven mortality by a median of 1.02 ± 0.15 % saturation (i.e. 0.07 ± 0.01 mg O_2 L^{-1} $ºC^{-1}$). Assessment of the impact of the 4 ºC warming expected during the 21st Century on the survival time and the threshold oxygen concentrations for mortality of benthic macrofauna using the average Q_{10} values for median survival time (3.01 ± 0.29) and median lethal oxygen concentration (2.09 ± 0.20) derived here predict that survival times will decrease by a mean of 35.6 % under hypoxia and that the threshold oxygen concentrations for high mortality to occur will increase by, on average, 25.5 % in a 4 ºC warmer ocean. Hence, ocean warming is expected to increase the vulnerability of benthic macrofauna to reduced oxygen concentrations, increasing the mortality of benthic fauna and greatly extending the area of coastal ecosystems affected by hypoxia-driven mortality.

Introduction

Global warming is forecasted to lead to increase the mean global temperature by 1.8 to 4 ºC 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). Dissolved oxygen is the property that has changed more drastically in a shorter period of time in the marine environment (Diaz & Rosenberg 1995; Diaz 2001). Oxygen deficiencies have increased in frequency, duration, and severity in the world´s coastal areas during the last decades (Diaz & Rosenberg 2008). As a consequence hypoxia is emerging as a major threat to marine coastal biodiversity (Vaquer-Sunyer & Duarte 2008). Environmental factors, such as the presence of sulphide (Vaquer-Sunyer & Duarte 2010); hypercapnia and low pH (Boleza et al. 2001; Rosa and Seibel 2008), which are increasing with the increased $p\mathrm{CO}_2$ and acidification of ocean waters (Caldeira & Wickett 2003; Zeebe *et al.* 2008), have been shown to enhance the sensitivity of marine organisms to hypoxia. Warming may also contribute to exacerbate hypoxia and its consequences for marine life.

Temperature is a key factor controlling the extent of hypoxia (Conley *et al.* 2007), 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). Stramma et al. (2008) documented the vertical expansion of the intermediate-depth low oxygen zones in the eastern tropical Atlantic and the equatorial Pacific during the past 50 years. The hypoxic boundary has shoaled up to 90 m in the Californian Current System (Bograd et al. 2008). The oxygen content of the Oxygen Minimum Zones (OMZ) has been documented to decline in the tropical Pacific, Atlantic and Indian Oceans (Stramma *et al.* 2009; Stramma et al. 2010). The expansion and shoaling of OMZ have been attributed to ocean warming (Keeling and Garcia 2002; Whitney et al. 2007).

The effects of climate change on water temperature are complex and modulated by multiple factors such as changes in wind patterns with subsequent changes in surface currents, circulation and mixing processes. Severe inner-shelf hypoxia off Oregon coast was documented in 2002 (Service 2004). The formation of this new hypoxic area was attributed to deviations in the circulation of the California Current System (Grantham et al. 2004) that further reflect large-scale wind stress anomalies present over the northeast Pacific in 2002 (Murphree et al. 2003). Increasing temperature can produce intensification of coastal upwelling (Bakun 1990; Bakun and Weeks 2004) with a subsequent oxygen decline in bottom waters bellow the upwelling system when low grazing pressure allow the sinking and subsequent respiratory decomposition of primary production (Bakun and Weeks 2004). In these areas the upwelling of cold waters can lead to cooling, instead of warming, of seawater. Despite this decrease of water temperature in regions with intensified upwelling, there is a general trend toward a global warming of the upper ocean. Lyman et al. (2010) reported significant warming of the upper ocean (from 0 to 700m depth) at global scales over the past 16 years. Recent observational surveys have shown significant warming of ocean bottom-waters (Fukasawa et al. 2004; Masuda et al. 2010). The water temperature in shallow bays from the Swedish West coast has also been reported to have increased (Cossellu and Nordberg 2010). The seawater temperature at the West Mediterranean Sea has increased between 0.12 and 0.5ºC from 1948 to 2005 in the upper layers (0 to 200 m), between 0.05 and 0.2 ºC from 1948 to 2000 in the mid layer (from 200 to 600 m depth) and between 0.03 and 0.1ºC from 1948 to 2005 in the deep water (from 1000 to 2000 m) (Bladé et al. 2010). A coastal site (85 m depth) in the continental shelf of the Catalonian Sea (West Mediterranean) sampled weekly exhibited intense warming trends at all depths ranging from 0.03 to 0.04ºC/year along the period from 1974 to 2001(Vargas-Yanez et al. 2005). Hence, despite variable effects at specific locations, there is a well documented tendency for seawater temperature to increase over the top 700 m, where most hypoxic events have been documented, at the global scale.

Increasing temperature diminishes oxygen solubility (Carpenter 1966; Garcia & 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 (Iriberri 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, within the limits imposed by resources (light, CO_2 and nutrients, and oxygen concentration, respectively), 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). On the basis of this differential response, Harris et al. (2006) predicted that an hypothetically four degree increase in the summer water temperature of a north-eastern Atlantic estuary will result in a 20% increase in net primary production and a 43% increase in heterotrophic metabolism, resulting in a 16% decrease of the P:R ratios and an increasing likelihood of system heterotrophy. These predictions, however, may be conservative, as they refer to specific metabolic rates but do not consider possible effects of warming on autotrophic and heterotrophic biomass. Müren *et al.* (2005) showed that the heterotrophic to autotrophic biomass ratio increased 5 times and the production to respiration ratio decreased six times when temperature was raised from 5 to 10ºC in experimental mesocosms. A decrease in ecosystem P:R ratios with increasing temperature could result in a net decrease in oxygen concentration, increasing the frequency and severity of hypoxic events. 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. Because the range of species where experimental assessment of temperature effects on thresholds of hypoxia is limited, the generality of the conclusions reached here must be tested further when data for species not included here become available.

Methods

We searched the Web of Science and Scholar Google for reports of hypoxia using the keywords ‘hypoxia’, ‘marine’, ‘benthic’ and ‘sea’, and their combinations to guide the search. This search delivered more than 6000 published reports of responses of benthic marine organisms to hypoxia, which were then examined further for the availability of experimental assessments of responses to reduced oxygen concentration that included temperature and/or evaluated them at different experimental temperatures. We also searched the list of papers cited in those retrieved by the search. This more restricted search delivered a total of 363 experimental assessments examining the median lethal time (LT_{50}), representing the statistically derived time interval at which 50% of a given population dies after exposure to low O_2 levels, involving 108 different species of marine benthos; and a total of 213 experimental assessments examining the median lethal concentration (LC_{50}), representing the statistically derived O_2 concentration at which 50% of the organisms in a given population die, involving 39 different species of marine benthos. Data on the experimental water temperature were derived from the paper, and where they were only reported in graphics were extracted digitalizing data using Graph Click 2.9.2 software.

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 LC_{50} (% sat. and mg O_2 L^{-1}) and LT_{50} (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.

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 (LT_{50}, 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 (LC_{50}, % saturation and mg O_2 L^{-1}) was assessed (Fig 1b,c). The aim of this ample comparison is to test for evidence of a temperature-dependence in the thresholds of hypoxia for coastal benthic organisms. The experiments compiled include a diversity of procedures and species, which may add variability to the analysis, contributing to the residual variability.

Examination of the relationship between LT_{50} and experimental temperature showed that the range of LT_{50} values observed declined with increasing temperature, with most experiments conducted showing relatively low LT_{50} 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 LT_{50} with increasing temperature (Fig 1a). The 95% quantile regression, estimating the temperature dependence of the maximum LT_{50} expected for a given water temperature, indicated a decrease in the maximum LT_{50} by 63.62 ± 19.10 hours per each degree of temperature increase, whereas the 5% quantile regression, estimating the temperature dependence of the minimum LT_{50}, showed only a decrease by 0.45 ± 0.31 hours (27 minutes) for each degree Celsius increase. The median LT_{50} declined by 3.95 ± 1.67 hours for each degree Celsius of temperature increase (Fig 1a). The variability in LT_{50}, 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 ºC) to 0 to 47.5 hours at the high end (30 ºC, Fig. 1a).

The intercepts and slopes of the regressions between LT_{50} and experimental temperature showed significant differences among taxonomic groups. No significant relationship between LT_{50} 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 ^{o} C^{-1}, $R^2 = 0.99$, $p < 0.007$, N = 3), whereas molluscs showed a much smaller decrease in survival time (41.90 ± 5.46 hours ^{o} C^{-1}, $R^2 = 0.25$, $p < 0.0001$, N = 189) with warming.

The relationship between LC_{50} (% 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) mg O_2 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) mg O_2 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) mg O_2 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% interquantile range, increased with increasing temperature from 0.00 to 15.50 % saturation (i.e. 0.00 to 2.24 mg O_2 L^{-1}) at the lower end of marine temperature (0 ºC) to 11.63 to 98.00 % oxygen saturation (0.80 to 6.74 mg O_2 L^{-1}) at the high end (30 ºC, Fig.1b,c).

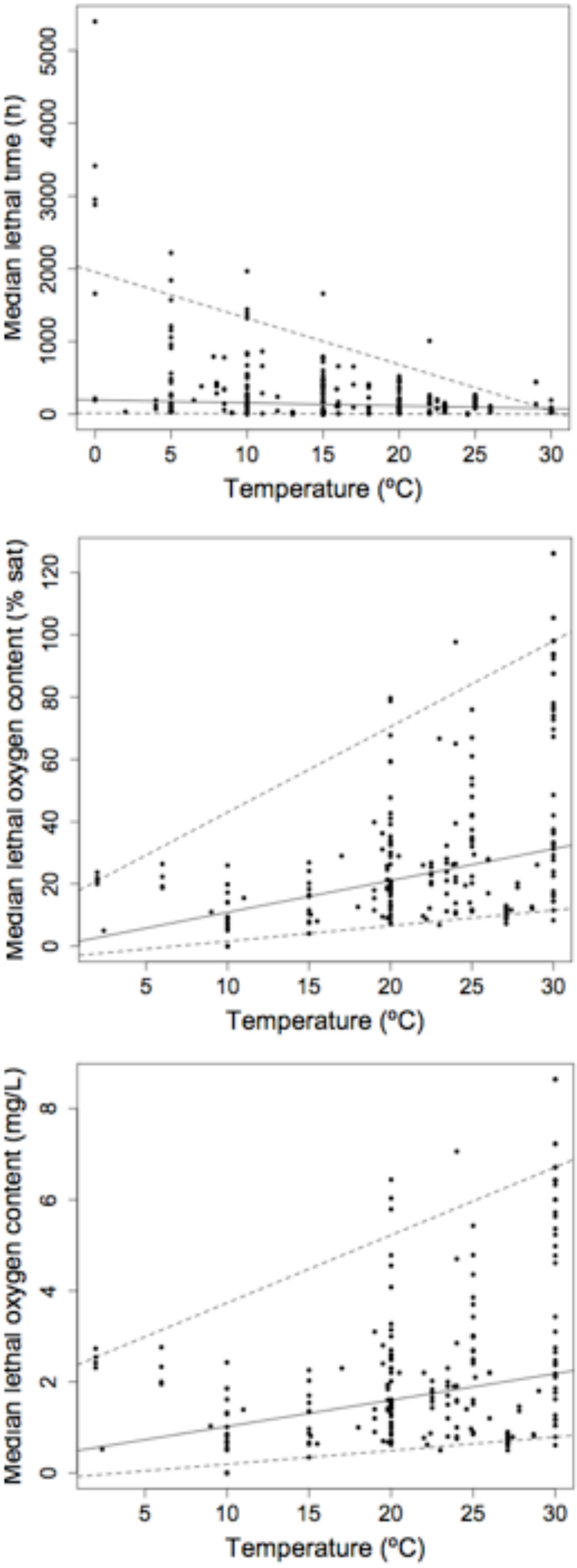

Figure 1. (a) The relationship between the median lethal time (LT50, h) and water temperature for the different experiments. The solid line represents the fitted regression for the median or the 50% quartile [LT50 (h) = 194.70 (±34.04)-3.95 (±1.67)* temperature; N=363, $P<0.03$]. The dashed lines represent the fitted regression for the 95% quantile [LT50 (h)=1956.25 (±430.54)-63.62 (±19.10) * temperature; N =363, $P<0.001$] and the 5% quantile [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% quantile (LC50 (% sat.)=15.50 (±8.99)+2.75 (±0.47)*temperature; N=213, $P<0.0001$) and the 5% quantile (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, $mgO_2\ L^{-1}$) and the water temperature for the different experiments. The solid line represents the fitted regression for the median or the 50% quartile [LC50 ($mgO_2\ L^{-1}$)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 (mgO_2L^{-1}) = 2.24 (±0.68)+0.15 (±0.04)*temperature; n=212, $P<0.0001$] and the lower 5% quartile [LC50 (mgO_2L^{-1})=-0.10 (±0.32) +0.03 (±0.01)* temperature; N=212, $P<0.02$] (see Annex 7 at http://imedea.uib-csic.es/users/raquel/phD_Annexes/ for data sources).

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 $^{o}C^{-1}$, $R^2 = 0.26$, $p < 0.0001$, N = 125; i.e. 0.15 ± 0.03 mg O_2 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 $^{o}C^{-1}$, $R^2 = 0.40$, $p < 0.0007$, N = 26; i.e. 0.09 ± 0.02 mg O_2 L^{-1}, $R^2 = 0.37$, $p < 0.001$, N = 26).

We found a total of 189 published experiments involving 21 species from 5 different taxonomic groups of benthic macrofauna where the median lethal time (LT_{50}, 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.

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 (± 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 ($\frac{LT_{50\,T\,\min}}{LT_{50\,T\,\max}}$) and the temperature increase (ΔT, ° C), as described by the fitted regression equation:

$$\frac{LT_{50\,T\,\min}}{LT_{50\,T\,\max}} = 0.81 + 0.21\ (\pm 0.03)\ \Delta T\ (^{o}C)$$

$(R^2 = 0.19,\ p < 0.0001)$

Calculated Q_{10} values for the change in LT_{50} (h) with increasing temperature showed a broad range of values with an average (± 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

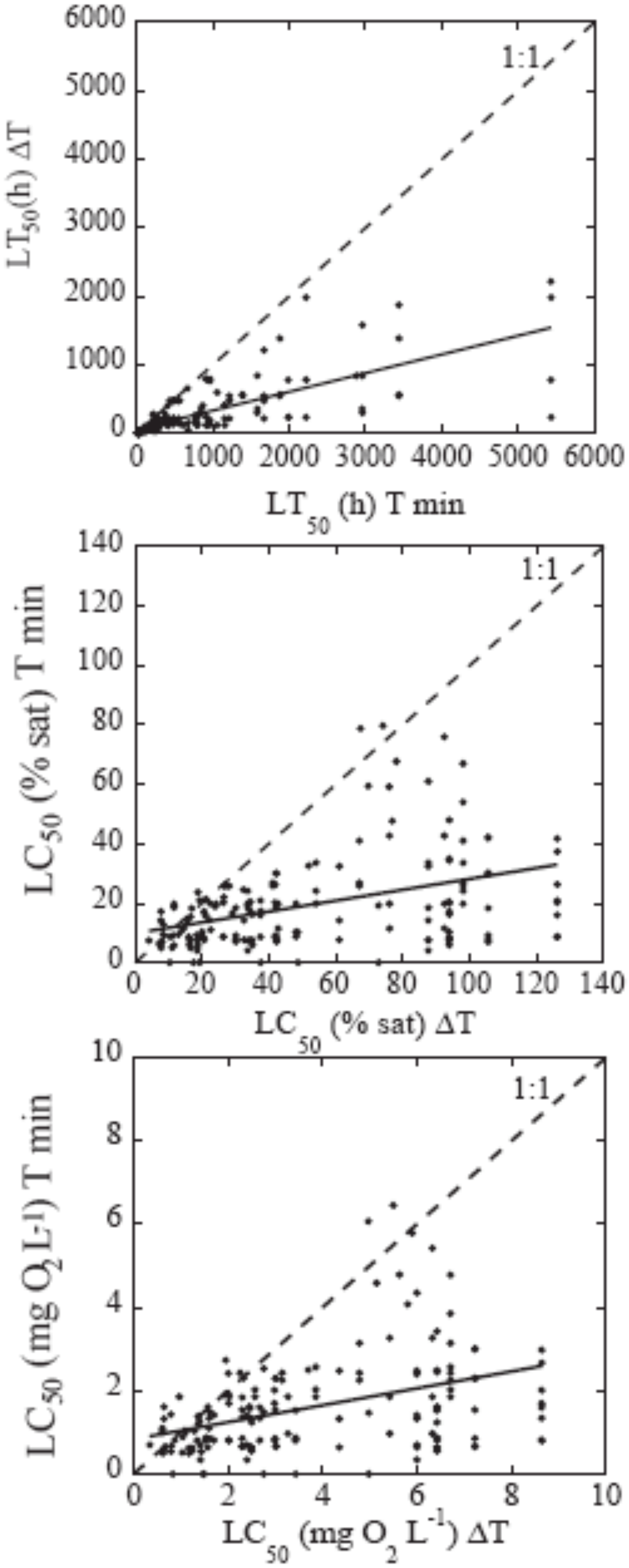

Figure 2. (a) The relationship between the median lethal time at increased temperature (LT50ΔT) and median lethal time at lower temperature (LT50) (units: h). LT50ΔT (h)=80.04 (±22.68)+0.26 (±0.02)*LT50 (h). (R^2=0.54, P<0.0001) n5189. The solid line represents regression line and dashed line represents the line 1:1. (b) The relationship between the median lethal concentration at one temperature (LC50 Tmin) and median lethal concentration at increased temperature (LC50ΔT) (units: % oxygen saturation). LC50 Tmin (% oxygen saturation)=9.85 (±2.01) + 0.18 (±0.03)* LC50ΔT (% 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 (LC50 Tmin) and median lethal concentration at increased temperature (LC50ΔT) (units: mgO_2 L^{-1}). LC50 Tmin (mgO_2 L^{-1})=0.84 (±0.16)+0.20 (±0.04) * LC50ΔT (mgO_2 L^{-1}). (R^2=0.16, Po0.0001) N=165. The solid line represents regression line and dashed line represents the line 1:1 (see Annex 8 at http://imedea.uib-csic.es/users/raquel/phD_Annexes/ for data sources)

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 (± SE), 81.7 ± 3.1 % and 79.9 ± 4 % when temperature was elevated in terms of % saturation (Fig. 2b) and concentration (mg O_2 L^{-1}, Fig. 2c), respectively. Calculated Q_{10} values for the change in LC_{50} with increasing temperature showed an average (± 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 mg O_2 $L^{-1,}$ 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 Q10 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 ($F = 5.16$, $p < 0.006$).

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 (LC_{50}, % 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.

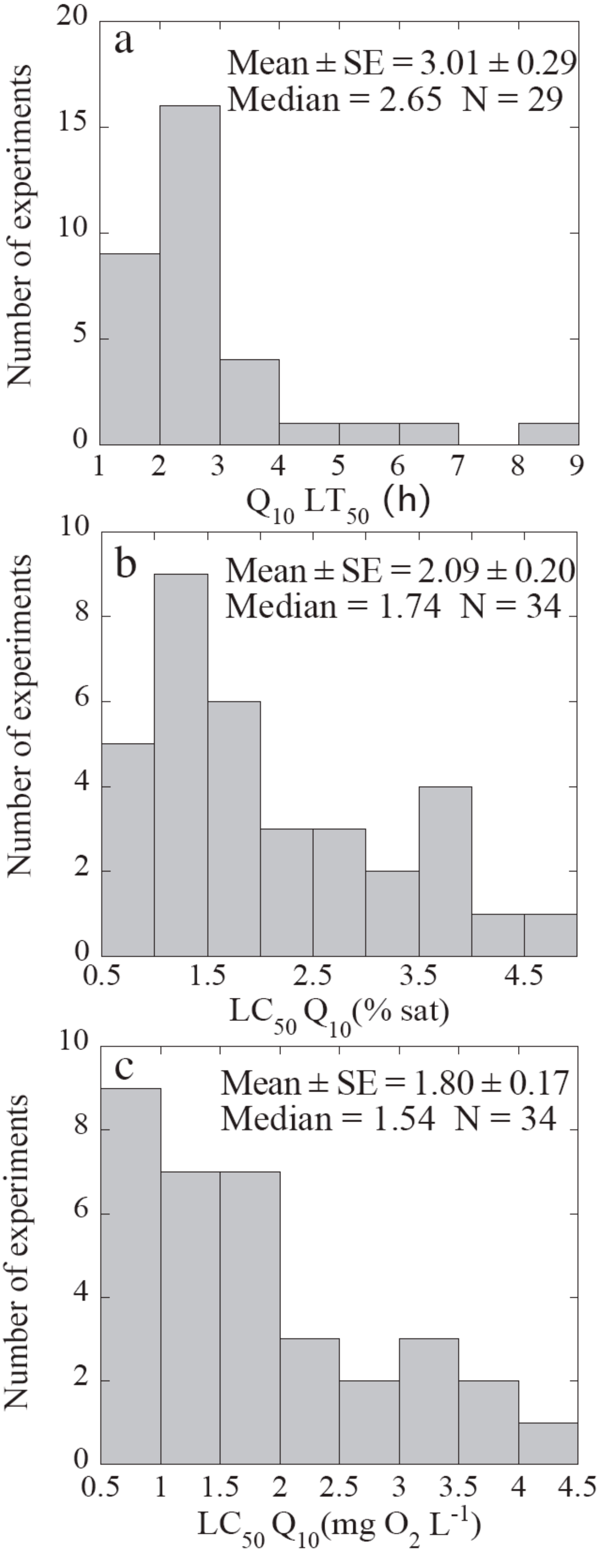

Figure 3. Frequency distribution for Q_{10} values for median lethal time (a) and for median lethal oxygen concentration in % sat. (b) and in mg O_2 L^{-1} (c). Data on Q_{10} for median lethal time calculated from (Gamble, 1970; Dries & Theede, 1974; Shumway et al. 1983; Oeschger & Theede, 1986; Stickle et al. 1989; Brooks et al. 1991; Johnson & McMahon, 1998; de Zwaan et al. 2001) and on Q_{10} for median lethal oxygen concentration calculated from (Shimps & Rice personal comment; Vargo & Sastry, 1977; Stickle et al. 1989; Schurmann & Steffensen, 1992; Hoback & Barnhart, 1996; Plante et al. 1998; Miller et al. 2002; Cerezo & Garcia, 2004; Ishibashi et al. 2005; Shimps et al. 2005; Goodman & Campbell, 2007).

Examination of the relationship between LC_{50} (% sat.) and water temperature showed that the range of median lethal O_2 concentration increased significantly with increasing water temperature, suggesting that the relationship between LC_{50} (% 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. Conversely, some tolerant species may benefit from reduced tolerance of predators, as the case of the quahog clam (*Mercenaria mercenaria*) that gained refuge from its less tolerant predators that are either excluded or less effective under hypoxia (Altieri 2008). 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 O_2 concentration of 0.24 mg O_2 L^{-1} per each degree Celsius of warming, and an even steeper increase for the 95% quantile (0.31 ± 0.06 mg O_2 L^{-1} $^{o}C^{-1}$). 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 LT_{50} (h) and LC_{50} (% 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 Q_{10} values describing the temperature-dependence of the thresholds of hypoxia for benthic macrofauna are comparable to those describing the temperature dependence of respiration rates (Q_{10} values around 2 - 3, cf. Neori & Holm-Hansen 1982; Raven & 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 ºC and 4 ºC warming, respectively. For a oyster (*Crassostrea virginica*) living in waters with 30 psu and 20ºC, this reduction means a decrease in its survival time from 20 to 10 days with a 4ºC warming and to 14 days with a 1.8ºC 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 ºC, and 4 ºC, respectively. The consequences for an oyster living at 20ºC 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 O_2 l^{-1}) to 27 % or 23 % saturation (i.e. 1.95 or 1.71 mg O_2 l^{-1}) with warming of 4 or 1.8ºC respectively.

Three species showed an increase in survival time with warming, the bivalve *Corbicula fluminea* (Johnson and McMahon 1998), the polychaeta *Nephthys ciliata* (Dries & Theede 1974) and the crustacean *Corophium arenarium* (Gamble 1970). The cause for their decrease in survival at low temperatures is probably due to thermal stress, rather than hypoxia, because the experimental temperatures tested were not within the thermal niche of the species, as *Corbicula fluminea*, for example, is a warm-water specie (Johnson & McMahon 1998). When organisms are maintained outside their thermal optimal oxygen levels in body fluids can decrease, as a consequence of excessive oxygen demand at high temperatures or insufficient aerobic capacity of mitochondria at low temperatures (Portner 2001). In the case of the crustacean *Corophium arenarium* the difference in survival time was very small (0.83 h or 6% lower) for experiments made at 15ºC and 10ºC, compared with the differences in survival time measured at 20ºC and 15ºC (5.52 h, 39%) or between 10ºC and 5ºC (19.27 h, 60%). Only 11 experiments from a total of 165 belonging to 4 different species showed a higher LC_{50} at low temperatures than at warmer ones. These species were the Atlantic cod *Gadus morhua*, the crabs *Callinectes sapidus* and larval stages of *Cancer irroratus* and the gastropod *Thais haemastoma.* Two of these experiments were made to assess changes in the oxygen requirements of the Atlantic cod *Gadus morhua* with warming (Plante *et al.* 1998), two in the crab *Callinectes sapidus* (Stickle *et al.* 1989), 3 in the gastropod *Thais haemastoma* (Stickle et al. 1989), and four in larval stages of the crab *Cancer irroratus* (Vargo and Sastry 1977). In the case of the third and fifth zoea larval stage of the crab *Cancer irroratus*, the hypoxia tolerance decreased at 10ºC, indicating a failure in metabolic adaptation to this lower temperature, as their culture temperature was 15ºC (Vargo and Sastry 1977). The published studies revealed either no effect of temperature on hypoxia tolerance of Atlantic cod (*Gadus morhua*) or decreasing tolerance with increasing temperature. The Atlantic cod (*Gadus morhua*) did not show measurable differences in survival under different temperatures ranging form 2 to 6ºC (Plante *et al.* 1998), but it showed decreasing hypoxia tolerance with warming in a later study where the temperature ranged from 2.4 to 17ºC (Schurmann and Steffensen 1992).

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 º 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 (Fig. 4). Hence, ocean warming is expected to increase the thresholds of hypoxia-driven mortality of benthic macrofauna. Provided that ocean warming is already documented to affect, in most areas, the top 700 m of the ocean (Lyman et al. 2010), further warming is expected to extend the area of coastal ecosystems affected by hypoxia-driven mortality, except in areas where ocean dynamics may buffer warming, such as areas where upwelling maybe intensified. As for present hypoxia, the extent of impacts will vary among taxa, depending on physiological strategies, life stages and motility, but will also depend on the capacity of microevolutionary process to increase the resistance of benthic organisms to hypoxia along the 21st Century.

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 4ºC 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

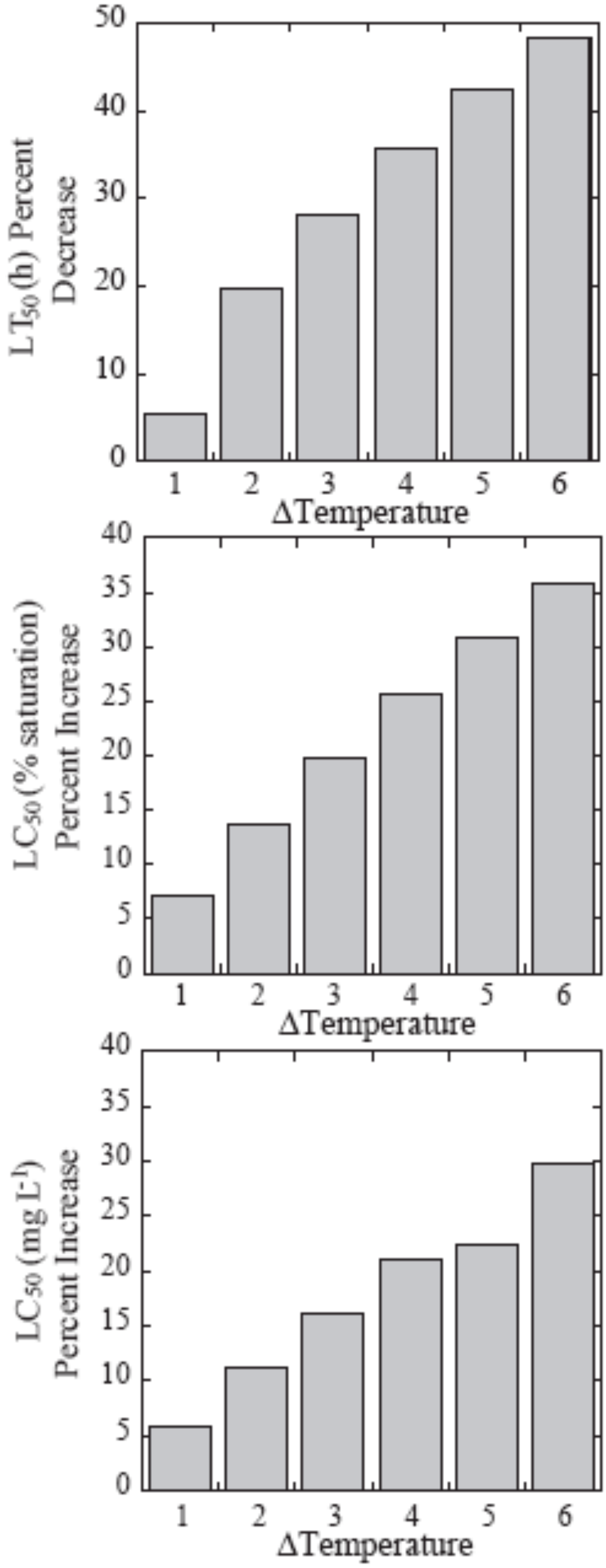

Figure 4. Changes in hypoxia thresholds calculated from Q_{10} values derived here. (a) Percentage of decrease of median lethal time expected with different water warming; (b) increase of the median lethal oxygen content expected for different water temperature increases in % sat.; (c) in mg O_2 L^{-1}.

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 & 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 & 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 ºC during summer months could practically eliminate suitable habitats for juvenile Atlantic sturgeon (*Acipenser oxyrhynchus*). 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 & Farrell 2008). Warming above the thermal window of the organisms can also trigger anaerobic metabolism (Portner & 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 $^{\circ}C^{-1}$ and by increasing the oxygen thresholds for hypoxia-driven mortality by a median of 1.02 ± 0.15 % saturation $^{\circ}C^{-1}$ (0.07 ± 0.01 mg O_2 L^{-1} $^{\circ}C^{-1}$) across the species for which evidence is available. Hypoxia is already expanding globally across coastal waters (Diaz & 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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