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Ocean acidification and hypoxia alter organic carbon fluxes in marine soft sediments

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Abstract

Anthropogenic stressors can alter the structure and functioning of infaunal communities, which are key drivers of the carbon cycle in marine soft sediments. Nonetheless, the compounded effects of anthropogenic stressors on carbon fluxes in soft benthic systems remain largely unknown. Here, we investigated the cumulative effects of ocean acidification (OA) and hypoxia on the organic carbon fate in marine sediments, through a mesocosm experiment. Isotopically labelled macroalgal detritus (¹³C) was used as a tracer to assess carbon incorporation in faunal tissue and in sediments under different experimental conditions. In addition, labelled macroalgae (¹³C), previously exposed to elevated CO₂, were also used to assess the organic carbon uptake by fauna and sediments, when both sources and consumers were exposed to elevated CO₂. At elevated CO₂, infauna increased the uptake of carbon, likely as compensatory response to the higher energetic costs faced under adverse environmental conditions. By contrast, there was no increase in carbon uptake by fauna exposed to both stressors in combination, indicating that even a short-term hypoxic event may weaken the ability of marine invertebrates to withstand elevated CO₂ conditions. In addition, both hypoxia and elevated CO₂ increased organic carbon burial in the sediment, potentially affecting sediment biogeochemical processes. Since hypoxia and OA are predicted to increase in the face of climate change, our results suggest that local reduction of hypoxic events may mitigate the impacts of global climate change on marine soft-sediment systems.

KEYWORDScarbon sequestration, climate change, enhanced CO₂, hypoxia, infauna, macroalgal detritus, multiple stressors, stable isotope

1 | INTRODUCTION

Marine sediments are key for the accumulation and burial of organic matter (Berner, 1982; Smith, Bianchi, Allison, Savage, & Galy, 2015). The input of organic detritus from the water column is one of the main sources of carbon to resident burrowing fauna, mediators of benthic pelagic exchange processes that in turn determine the fate of organic matter at the global scale (Middelburg,

2018; Snelgrove et al., 2018). These processes include direct metabolic carbon uptake and mineralization (Woulds et al., 2016), particle reworking and burrowing ventilation, which affect detritus availability to other biota (Kristensen et al., 2012; Snelgrove et al., 2018). Anthropogenic stressors, including global warming, ocean acidification (OA) and oxygen depletion, impact the structure and functioning of these communities, having thus the power to influence benthic–pelagic carbon fluxes (Godbold & Solan, 2013;

Laverock et al., 2013; Widdicombe et al., 2009). However, the influence of anthropogenic stressors on marine sediment carbon cycling remains largely unquantified (Keil, 2017).

Hypoxia (defined as oxygen concentration ≤ 2 ml of O_2/L ; Diaz & Rosenberg, 2008) has increased in many coastal areas worldwide, as a consequence of both natural and anthropogenic influences (Breitburg et al., 2018; Levin, 2018; Schmidtko, Stramma, & Visbeck, 2017; Vaquer-Sunyer & Duarte, 2008). Among anthropogenic stressors, eutrophication is one of the main drivers of coastal hypoxia. Enhanced nutrient loading to seawater stimulates algal biomass accumulation and the subsequent microbial degradation of organic matter to the seabed lowers oxygen levels (Reed & Harrison, 2016; Steckbauer, Duarte, Carstensen, Vaquer-Sunyer, & Conley, 2011). The intensity, duration and frequency of hypoxic events are expected to increase because of global warming, which is reducing O_2 solubility, whilst increasing primary production, thermally induced stratification and biotic respiration (Keeling, Körtzinger, & Gruber, 2010; Schmidtko et al., 2017). In addition to this chronic reduction in oxygen availability, acute sporadic oxygen depletion events can occur near the coastal seabed, following periods of intense autotrophic growth in surface waters, which are followed by fast, intense deposition of decaying phyto- and zooplankton on the sediment surface (Tait et al., 2015; Zhang et al., 2015). The effects of hypoxia on benthic community structure and functioning are well known (Levin et al., 2009; Middelburg & Levin, 2009; Zhang et al., 2010). For instance, hypoxia can result in shallower infaunal activity within the sediment (Riedel et al., 2014), metabolic depression and, over time, decreased body size (Diaz & Rosenberg, 1995), ultimately altering sediment biogeochemistry (Middelburg & Levin, 2009). Hypoxia can also restrict macrofaunal burrowing activity to superficial sediment layers, thus reducing the vertical, downward transport of material and increasing the proportion of organic matter degradation that occurs near the sediment surface (Middelburg & Levin, 2009). Finally, lower levels of aerobic respiration slow down carbon mineralization (Jessen et al., 2017; Woulds, Andersson, Cowie, Middelburg, & Levin, 2009; Woulds et al., 2007).

In addition to hypoxia, increased anthropogenic CO_2 emissions are driving up levels of atmospheric CO_2 , which in turn increases the rate of oceanic CO_2 uptake. Once dissolved in the surface ocean, this CO_2 drives a series of changes and reactions in the marine carbonate system and these chemical changes are collectively known as OA (Doney, Fabry, Feely, & Kleypas, 2009). Under the current rate of CO_2 emission, seawater CO_2 concentrations are expected to increase from ~ 385 to ~ 700 – $1,000$ ppm by the end of the century, based on the fifth IPCC Assessment Report's Representative Concentration Pathway (RCP) 8.5 (Riahi et al., 2011; Stocker et al., 2013). In addition, in coastal hypoxic regions, with a strong vertical stratification and high nutrient loadings, levels of seawater CO_2 already exceed those predicted by the end of the century ($pCO_2 > 1,000$ μatm), as heterotrophic degradation of organic matter increases metabolic CO_2 release because of respiratory processes (Cai et al., 2011; Melzner et al., 2012). Thus, much higher CO_2 values are expected to occur concomitantly with hypoxia in many shelf and estuarine

regions worldwide, as a consequence of climate change (e.g. warming and OA; Breitburg et al., 2018; Carstensen & Duarte, 2019).

The potential for elevated CO_2 to negatively impact a wide variety of marine organisms and biological processes is well documented (Gaylord et al., 2015; Kroeker et al., 2013; Sunday et al., 2016; Vargas et al., 2017). However, the impacts of elevated CO_2 on the structure and functioning of soft-sediment ecosystems remain less understood (Godbold & Solan, 2013; Keil, 2017; Laverock et al., 2013). Although elevated CO_2 does not always cause mortality to infaunal species, a trade-off between the maintenance of core activities (e.g. respiration and growth) and locomotion, tightly linked to fauna particle transport (Queirós et al., 2013), might be expected, resulting from the allocation of additional energy (i.e. ATP) to physiological stress response pathways (Pan, Applebaum, & Manahan, 2015; Widdicombe & Spicer, 2008; Wood, Spicer, & Widdicombe, 2008). In addition, elevated CO_2 can indirectly alter the relationship between consumers and organic matter sources, modifying the nutritional quality of food (i.e. higher C:N ratio), thus affecting carbon uptake (Duarte et al., 2016; Kamyra, Byrne, Mos, Hall, & Dworjanyn, 2017; Poore et al., 2013; Rossoll et al., 2012).

Enhanced CO_2 concentration in seawater can further alter sedimentary carbon cycling in marine sediments through changes in primary production and respiration (Engel et al., 2013; Molari et al., 2018; Piontek et al., 2013; Riebesell et al., 2007). Elevated CO_2 may stimulate primary production (Engel et al., 2013), but reduce organic carbon remineralization due to changes in C:N ratio (Riebesell et al., 2007), potentially enhancing organic carbon sequestration in sediments. Elevated CO_2 may reduce carbon burial through the stimulation of organic matter microbial degradation (Grossart, Allgaier, Passow, & Riebesell, 2006; Piontek et al., 2013) and faunal respiration (Molari et al., 2018). These contrasting effects of elevated CO_2 on bulk organic carbon may be the result of complex pathways of impacts on benthic communities and carbon sediment stores, potentially resulting in cumulative neutral impacts and challenging predictive frameworks (Zark, Riebesell, & Dittmar, 2015).

Although coastal areas with low O_2 and elevated CO_2 have been largely documented worldwide and will continue to increase under future climate conditions (Melzner et al., 2012), the vast majority of studies have focused on the effects of these stressors in isolation. A few recent studies that have examined hypoxia and elevated CO_2 together have reported either additive or synergistic effects of hypoxia and elevated CO_2 on the survivorship, development and growth of different species of marine invertebrates (Gobler & Baumann, 2016; Gobler, Depasquale, Griffith, & Baumann, 2014; Steckbauer et al., 2015). However, to date, no study has investigated the effects of both stressors simultaneously on infaunal communities and the carbon fluxes they mediate.

Here, using a 4 week mesocosm study, we investigated the compound effects of hypoxia and elevated CO_2 on the fluxes of organic carbon in soft sediments, considering faunal-driven benthic-pelagic processes. Using isotopically labelled macroalgal detritus (^{13}C), a common source of organic matter supplied to the coastal ocean (Krause-Jensen & Duarte, 2016; Queirós et al., 2019), we traced

organic carbon uptake of a pulsed supply into sedimentary faunal tissues and organic carbon stores under different oxygen availability and CO₂ levels. We predicted that the combined effects of elevated CO₂ and hypoxia could significantly reduce the faunal uptake of algal detritus, by causing metabolic depression in marine invertebrates (Levin et al., 2009; Widdicombe et al., 2009). Alternatively, elevated CO₂ could increase resource uptake by fauna (Queirós et al., 2015; Thomsen, Casties, Pansch, Kortzinger, & Melzner, 2013), due to increasing energetic demands associated with physiological responses under OA (e.g. protein synthesis, pH homeostasis, calcification; Pan et al., 2015; Ramajo, Pérez-León, et al., 2016; Stumpp et al., 2012), thus counteracting the negative effects of hypoxia on feeding activities. In addition, the increase in sediment carbon incorporation expected under hypoxic conditions (Jessen et al., 2017) could be dampened by elevated CO₂, possibly stimulating microbial degradation of algal detritus (Grossart et al., 2006; Piontek et al., 2013).

Moreover, in order to assess whether OA could alter organic carbon cycling directly (e.g. metabolic processes) or indirectly (e.g. modification of food quality), we carried out an independent experiment, where isotopically labelled macroalgae (¹³C), pre-exposed to elevated CO₂ for 10 days, were used as a tracer to assess the organic carbon uptake by fauna and sediments, when both sources and consumers were exposed to OA. Elevated CO₂ could increase the C:N ratio of algal detritus (Mercado, Javier, Gordillo, Niell, & Figueroa, 1999; Stiling & Cornelissen, 2007), possibly resulting either in a decrease of carbon uptake by fauna, due to lower organic matter palatability (Duarte, Navarro, Acuña, & Gómez, 2010; Kamyra et al., 2017), or in increased consumption of less nutritional food; Cruz-Rivera & Hay, 2001; Duarte, Acuña, Navarro, & Gómez, 2011). An increase in C:N ratio of algal detritus under elevated CO₂ condition could also increase the organic carbon burial in the sediment, possibly due to lower organic matter remineralization (Riebesell et al., 2007).

2 | MATERIALS AND METHODS

2.1 | Sediment and macroalgal collection and preparation

Sediments were collected on board of the Plymouth Marine Laboratory's RV Quest, at Station L4 (50°13'22.7"N, 4°11'23"W, also known as Hilmar's Box), located about 13 km southwest of Plymouth, in the Western English Channel. L4 is one of the most comprehensively studied coastal systems in the world, having been monitored routinely for over 100 years, generating a wide range of environmental and biological benthic–pelagic observations which are used, for example, by the European Union's Water Framework Directive (Smyth et al., 2015). The site is representative of the vast majority of shelf environments around the world and, at present, neither hypoxia nor acidification is a regular occurrence in this system (publicly available data at <http://www.westernchannelobservatory.org.uk>, not shown). Phytoplankton blooms at L4 are generally observed in spring and autumn, representing the main source of organic supply, together with macroalgal detritus, at the

seabed (Queirós et al., 2019; Smyth et al., 2015; Widdicombe, Eloire, Harbour, Harris, & Somerfield, 2010). During summer months, this site is generally characterized by thermal stratification and inorganic nutrient depletion in the surface water, suggesting N-limitation of primary production (Smyth et al., 2015). The seawater pCO₂ at the seabed has been shown to vary between 351 and 432 μatm, with a pH value always above 8.0 throughout the year (Kitidis et al., 2012). This site is generally not exposed to seasonal hypoxic events. A significant reduction of oxygen levels below the thermocline has been recorded during the summer of 2012, probably due to the largest and long-lasting phytoplankton bloom recorded locally over the past 20 years (Smyth et al., 2015; Tait et al., 2015; Zhang et al., 2015).

On 16 March 2016, 22 cores were collected from the soft-sediment bed of the benthic monitoring site of the L4 station, using six separate deployments of a 0.1 m² box core, at about 50 m depth. Seawater temperature (~10.5°C) and dissolved oxygen (~270 μM) at the seabed, during sampling day, are reported in Queirós et al. (2019). On retrieval to the deck, sediment with resident fauna and overlying water were immediately subsampled from each box core by pushing a maximum of four acrylic core tubes (10 cm diameter × 30 cm high) to a depth of approximately 12 cm. This method allows the preservation of the structural integrity of sediment in each core tube (Evrard et al., 2012; Queirós et al., 2019; Woulds et al., 2016), which is essential to maintain as much as possible ongoing sedimentary gradients and ecosystem processes (Stocum & Plante, 2006). The core tubes were equipped with oxygen sensor spots (PreSens), previously attached to the inner wall of the cores with silicone glue, just above the sediment surface (see below). Each core was, then, gently removed from the box core and capped at the bottom with a PVC lid fitted with an O-ring, further sealed by a plastic cap, which was glued to the core with biological grade silicon (Gold Label, Huttons Aquatic Products). The top of each core was sealed with an acrylic lid, onto which the tubing for an airstone sitting near the surface of the water in the core had been fitted. All cores were placed in two water baths containing seawater from the collected site and covered with black plastic sheets during transport to Plymouth Marine Laboratory to reduce temperature changes. Once in the mesocosm laboratory at Plymouth Marine Laboratory, the core tubes were randomly allocated to two 1 m³ mesocosm tanks. The laboratory is a temperature-controlled room where air temperature is maintained such that aquarium water in the room follows the seasonal cycle of bottom water at the L4 station (Findlay, Kendall, Spicer, Turley, & Widdicombe, 2008; Queirós et al., 2015). The 1 m³ mesocosm tanks were used as water baths to ensure that base temperature and light (absence of) conditions experienced by each core tube were as similar as possible during laboratory exposures, and water was not circulated between individual (microcosm) sediment cores. Water in each core was aerated for 24 hr prior to start the experiment by use of the fitted airstones, which promoted a gentle flow inside the core without causing resuspension.

The macroalga *Laminaria digitata* was used as a labelled food source in our experiment. *Laminaria* spp., together with other macroalgal species, have been shown to occur as organic detritus

within the sediment at L4, and they are one of the organic matter sources preferentially assimilated by infaunal assemblages at the site (Queirós et al., 2019), as indeed potentially in much of the coastal ocean (Krause-Jensen & Duarte, 2016). In February 2016, individuals of *L. digitata* were collected by hand from the low intertidal rocky shore at Rame Head (50°18'41.11"N, 4°13'14.89"O; England). All individuals were immediately transported to the mesocosm facility at the Plymouth Marine Laboratory, where they were placed in a recirculating water system tank and kept at ambient CO₂ for approximately 10 days. The tank was lit by two LED strip lights, positioned at a distance of about 40 cm from the water surface. Algae were maintained under constant light to maximize growth. Seawater was collected from the Western Channel Observatory during the previous week to each of the exposures (pH: mean ± SE = 8.09 ± 0.01; salinity: mean ± SE = 36.25 ± 0.75). Ten days later, some individuals of *L. digitata* were transferred to a separate tank in which conditions were otherwise the same, except for elevated seawater CO₂ level, and held there for 2 weeks. The CO₂ level in this tank was used to create a low pH treatment (pH mean ± SE = 7.75 ± 0.07) and was in line with the Intergovernmental Panel on Climate Change 5th Assessment Report's Representative Concentration Pathway (RCP) 8.5 atmospheric CO₂ for the year 2100, the scenario in which emissions are highest, and which does not include specific climate mitigation targets (Riahi et al., 2011; Stocker et al., 2013). The elevated seawater CO₂, and the resultant lower pH, in this tank was achieved by using a premixed gas system modified from Findlay et al. (2008). Briefly, the enrichment was achieved by mixing pure CO₂ gas with CO₂-free air using flow meters and mixing vessels, monitored with a CO₂ analyser (820, Li-Cor). The water bath with the low pH water was covered with sealed plastic sheets in order to insulate the tank's atmosphere from the laboratory atmosphere, allowing CO₂ in seawater and the air above it to equilibrate.

Individuals of *L. digitata* from the two treatments were then transferred to two clear acrylic aquaria, filled with seawater at either ambient or elevated CO₂ levels. The seawater in these aquaria contained 200% ¹³C-enriched bicarbonate (98% ¹³C, Sigma Aldrich) to label algae, and allow its subsequent tracing within the sediment cores. The aquaria were sealed with clear acrylic lids and maintained under constant light and ambient temperature for 72 hr. Labelled algae were then rinsed with unlabelled seawater to remove adhering ¹³C-bicarbonate and stored at -78°C before freeze-drying. Algal detritus marked with ¹³C (~13.23% and 66.7%, respectively, for macroalgae labelled at ambient and elevated CO₂ levels) was then ground to a fine powder using pre-acid-washed and muffle-furnaced agate pestle and mortars before being added to the experimental cores (Evrard et al., 2012; Hunter, Ogle, O'connor, & El-Sabaawi, 2019). ¹³C labelling was used to enable tracing of carbon between source and sedimentary consumers, and the use of the same population of macroalgae is also necessary because of strong variations that occur within and across individuals, as well as different populations (Phillips et al., 2014). Carbon and nitrogen content in macroalgal tissue was analysed using an elemental analyser. C:N

ratio in macroalgae maintained at ambient CO₂ seawater was significantly lower than those at elevated CO₂ (20.103 ± 0.37% and 22.73 ± 0.45%, respectively; $t = -4.50$; $p = .024$, $n = 2$).

2.2 | Macrofauna and sediment organic carbon uptake experiment

The sedimentary core experiment was set up for 4 weeks to examine the separate and cumulative effects of CO₂ concentration [CO₂] (ambient vs. elevated CO₂) and oxygen concentration [O₂] (normoxia vs. hypoxia) on faunal and sediment incorporation of labelled algae, which was previously maintained at ambient CO₂. Four replicate cores were then randomly allocated to each experimental treatment. Treatments were achieved by: selecting the air-CO₂ mix bubbled in each sediment core (manipulated as before); whether or not a hypoxia event was simulated; which macroalgal detritus was added to which core. Seawater was not circulated between individual (microcosm) cores. Only three replicate cores were used to simulate control conditions (ambient CO₂, normoxia), due to loss of one core during field sampling. Four cores were also used to test the effects of elevated CO₂ on faunal carbon uptake using labelled algae that were pre-exposed to elevated CO₂. Three additional control cores were maintained at ambient seawater CO₂, oxygen concentration and without labelled algae, and used to determine the ¹³C background content in faunal tissue and sediment (see below). Two CO₂ treatments were established, as used with the macroalgae, to compare present-day (ambient) values with those expected by the end of the century under RCP 8.5. pH_{NBS} was measured every 2 days and the average values (±SE) for the ambient and elevated CO₂ treatments were 8.17 ± 0.01 and 7.65 ± 0.02, respectively. Seawater temperature and salinity were measured every 2 days, whilst alkalinity samples were collected weekly from each core and measured using an automated titrator (Apollo SciTech Alkalinity Titrator Model AS-ALK2). Carbonate system parameters were calculated from measured pH, alkalinity, temperature and salinity using CO2SYS program for Excel with constant from Mehrbach, Culberson, Hawley, and Pytkowicz (1973) and adjusted by Dickson and Millero (1987; see Table S1).

After 2 weeks from the start of the experiment, water mixing was interrupted and 0.115 ± 0.0002 g of ¹³C-labelled *L. digitata* (equivalent to a C addition of ~1 g C/m²; Woulds et al., 2016) was added to the overlying water of each core and allowed to settle to the sediment surface. Correspondingly, 0.113 ± 0.0003 g of ¹³C-labelled algae pre-exposed to elevated CO₂ were added in four cores exposed to elevated CO₂. Airflow was reinstated 1 hr later in all but the hypoxia treatment cores. In these, airflow was interrupted for 46 hr by sealing the lids (and their openings) to cores with silicone grease (biological grade, Gold Label). Oxygen concentration in the water column was measured using the oxygen sensor spots (PreSens) and a fibre-optic oxygen transmitter equipped with a computer to collect the data. The oxygen sensors consisted of an oxygen-permeable foil, in which a chemical luminescence reaction takes place. The photoluminescence lifetime of the luminophore

within the sensor was measured by pointing the fibre-optic oxygen transmitter towards the outside of the wall in which the sensor was glued. Before each measurement, a two-point calibration was performed in all spot sensors, following manufacturer recommendation (0% and 100%). The 0% oxygen saturation was calibrated by adding sodium sulphide to distilled water. Seawater was, then, aerated with ambient air and stirred for 20 min to avoid oversaturation. At this point, it was used in the calibration as the 100% dissolved oxygen solution. We used the definition of hypoxia as oxygen levels of ≤ 2 mg/L (Diaz & Rosenberg, 2008), which hypoxia treatment cores reached after 46 hr. The cores were monitored using optodes, so that oxygen depletion was not extreme for too long. The average oxygen saturation of each treatment was $103.12 \pm 0.545\%$ and $18.74 \pm 3.08\%$, which correspond to $[O_2] = 10.20 \pm 0.446$ mg/L and $[O_2] = 1.794 \pm 0.294$ mg/L, respectively, for normoxia and hypoxia treatments.

All experiments were carried out in the dark and the incubations were terminated after 4 weeks from the start of the experiment. The duration of the experiment was appropriate to ensure that isotopic signal in traced carbon could be detected in primary consumers, whilst reducing the changes of complexity in measured response variables as the labelled detritus is cycled by subsequent consumers within the sedimentary food web (Middelburg, 2014; Queirós et al., 2019).

2.3 | Sample collection and analysis

At the end of the experiment (13 April 2016), the cores were processed for stable isotope analyses of organic carbon content in faunal tissue and sediment. For each core, sediment was sectioned into 0–2, 2–6 and 6–10 cm depth layers using a custom-built sediment slicer. Each layer was subsampled for the analysis of $^{13}C_{org}$ content in sediment, using a syringe that fitted tightly into a 50 ml falcon tube, and immediately frozen at $-20^\circ C$ until processing. The sediment remaining from each layer was used for the determination of $^{13}C_{org}$ incorporation into faunal tissue. Each sediment layer was sieved over a 0.5 mm sieve, and specimens were identified to the lowest taxonomical level possible using pre-combusted sorting equipment and then frozen in pre-weighed and pre-combusted petri dishes at $-80^\circ C$ until processing (within 2 weeks). Sediment and fauna samples were oven-dried at $60^\circ C$ for 48 hr. Each sample was then ground to a fine powder using agate pestle and mortars and, then, they were acidified by adding drops of 10% HCl, until all carbonates had been dissolved. All samples were oven-dried at $60^\circ C$ for 48 hr. Elemental and isotopic analyses of sediment and fauna samples were measured on constant flow isotope ratio mass spectrometers (Sercon model 20-20's, dual turbo pumped, CF/IRMS) connected to a Thermo EA1110 elemental analyser at OEA Labs (UK).

$^{13}C_{org}$ incorporation into fauna ($\% ^{13}C \text{ mg}^{-1} \text{ m}^{-2}$) and sediment ($\% ^{13}C$) was then calculated as the product of the excess ^{13}C (E) and C_{org} content in the fauna/sediment (expressed as percentage). E is the difference between the labelled fraction (F) of fauna/sediment sample and background fauna/sediment sample: $E = F_{sample} - F_{background}$, where

$F = ^{13}C / (^{13}C + ^{12}C) = R / (R + 1)$, where $R = (d^{13}C / 1,000 + 1) \times R_{VPDB}$, and $R_{VPDB} = 0.0112372$ (Sweetman et al., 2016). The carbon uptake by fauna was standardized for faunal biomass (mg DW) for each layer. Data from layers were summed to produce C uptake by fauna for each core. Background isotope information for sediment was taken from control cores (without labelled algae). Isotope signature for faunal invertebrates was unavailable from control cores, probably due to the low sample weight, so E was calculated using background F values from samples collected from the field at the same site in March 2016 (Queirós et al., 2019). $^{13}C_{org}$ content in faunal tissue and sediment samples was corrected for the fact that the added macroalgal detritus is not the 100% ^{13}C labelled: $C\text{-uptake} = ^{13}C \text{ incorporated} (\% ^{13}C) / \text{fractional abundance of } ^{13}C \text{ in algal detritus}$.

2.4 | Statistical analysis

The effects of $[CO_2]$ and $[O_2]$ on infaunal assemblages, within each sediment layer, were tested by means of a permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001), based on Bray–Curtis dissimilarity matrix of untransformed data. The model included two fixed factors: $[CO_2]$ (ambient vs. elevated CO_2) and $[O_2]$ (normoxia vs. hypoxia). In a separate analysis, the effects of $[CO_2]$ on the infaunal assemblages fed with algae previously exposed to enhanced CO_2 were tested using one-way PERMANOVA comparing the following treatments: control (ambient CO_2 /control algal detritus), elevated CO_2 /control algal detritus, elevated CO_2 /algal detritus exposed to enhanced CO_2 . Two-way analyses of variance (ANOVA), with $[CO_2]$ and $[O_2]$ as fixed orthogonal factors, were carried out on univariate data (total infaunal density, species diversity, fauna and sediment incorporation of labelled algae, previously maintained ambient CO_2). In a separate analysis, the effects of $[CO_2]$ on infaunal density, species diversity and faunal and sediment incorporation of algae, previously exposed to enhanced CO_2 , were tested using one-way ANOVA, comparing the same treatments described for one-way PERMANOVA analysis. Cochran's C-test was used to check for homogeneity of variances and, when necessary, data were log- or square root transformed. Student–Newman–Keuls (SNK) tests were used for comparison of the means.

3 | RESULTS

3.1 | Infaunal assemblage analyses

Animals (ind. per m^2) were mainly found in the uppermost 2 cm of the sediment (0–2 cm: 563.48 ± 92.41 ; 2–6 cm: 58.33 ± 12.88 ; 6–10 cm: 8.88 ± 4.79 ; data are mean \pm SE value averaged across experimental treatments; $n = 15$). A taxonomic list of infauna found within each sediment layer is reported in Appendix S1. There were no effects of $[CO_2]$ and $[O_2]$ on the structure of infaunal assemblages, within each sediment layer (Table S2). In addition, there were no differences in the infaunal assemblage composition between different sources of algal detritus or under ambient

and elevated CO₂ conditions, within each sediment layer (Table S3). In the upper 2 cm, echinoderms were the most abundant group with 56.18%, followed by polychaetes (27.29%), bivalves (5.79%), nematodes (4.96%), crustaceans (4.13%) and chelicerates (1.65%). In the 2–6 cm sediment layer, infaunal assemblage was dominated by polychaetes (85.72%), and the rest of the assemblage included Sipuncula (7.14%), cnidarians (3.57%) and bivalves (3.57%). Only one species of bivalve (*Lucinoma borealis*) was found in the deeper layer of sediment. Furthermore, there were no significant effects of [CO₂] and [O₂] on the total infaunal density and species diversity, within each sediment layer (Tables S4a and S5a). Finally, no differences were found in the total infaunal density and species diversity between different sources of algal detritus or under ambient and elevated CO₂ conditions, within each sediment layer (Tables S4b and S5b). The number of species and biomass per feeding modes within each sediment layer is reported in Appendix S2.

3.2 | Organic carbon assimilation in faunal tissue and sediment

There was a significant interaction between [CO₂] and [O₂] on the organic carbon uptake by fauna (Table 1a). At ambient CO₂, there were no differences in the organic carbon uptake by fauna between oxygen treatments, whilst, under elevated CO₂ level, the faunal carbon uptake was higher at normoxic than hypoxic conditions (Figure 1).

Sediment organic carbon enrichment was detected only in the 2–6 cm sediment layer (Figure 2), whilst there was no increase in the organic carbon compared to the background in the 0–2 and 6–10 cm sediment layers (Figure S1). ANOVA on the 2–6 cm sediment layer showed no significant effect of [CO₂] and [O₂] on the organic carbon incorporation in the sediment (Table 1a); however, there was a tendency ($F = 3.767, p = .08$) for the organic carbon burial to increase under hypoxia compared to normoxia, regardless of CO₂ treatments (Figure 2).

Source of variation	df	Fauna C-incorporation			Sediment C-incorporation		
		MS	F	p	MS	F	p
(a)							
[CO ₂]	1	0.0002	0.081	.783	0.0080	0.032	.863
[O ₂]	1	0.0017	0.788	.401	0.9533	3.767	.088
[CO ₂] × [O ₂]	1	0.0127	5.943	.041	0.0191	0.075	.791
Residual	8	0.0021			0.2531		
Transformation		log(x + 1)			log(x + 1)		
Cochran's test		p < .05			ns		
(b)							
Food quality	2	0.0040	1.214	.361	2.0836	5.455	.045
Residual	6	0.0033			0.3820		
Transformation		log(x + 1)			log(x + 1)		
Cochran's test		p < .05			p < .05		

TABLE 1 ANOVAs on the effects of (a) [CO₂] (ambient, elevated CO₂) and [O₂] (normoxia, hypoxia) and (b) food quality (ambient CO₂/control algal detritus, elevated CO₂/control algal detritus, elevated CO₂/algal detritus exposed to enhanced CO₂) on organic carbon incorporation in faunal tissue and in sediments

Bold values indicate significant results.

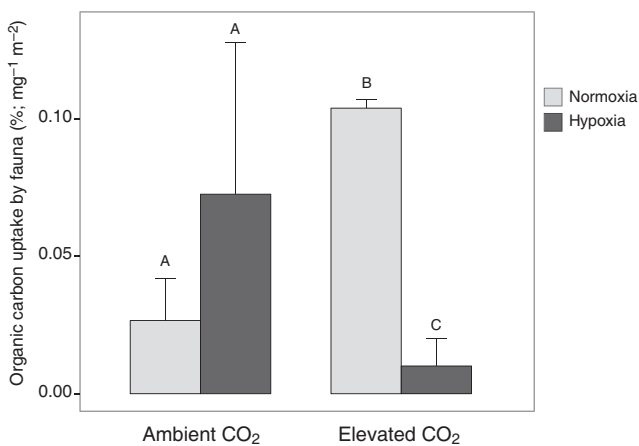


FIGURE 1 Organic carbon incorporation (mean ± SE) in fauna tissue (%; mg⁻¹ m⁻²) under different combinations of [CO₂] (ambient, elevated CO₂) and [O₂] (normoxia, hypoxia)

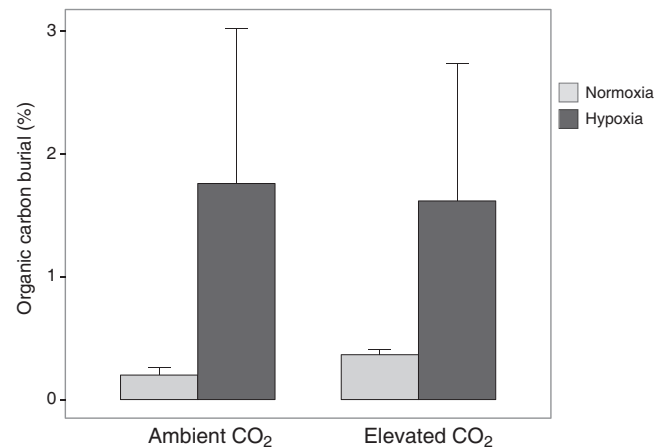


FIGURE 2 Organic carbon incorporation (mean ± SE) in sediment layers (%; 2–6 cm layer) under different combinations of [CO₂] (ambient, elevated CO₂) and [O₂] (normoxia, hypoxia)

FIGURE 3 Organic carbon incorporation (mean \pm SE) in fauna tissue (%; $\text{mg}^{-1} \text{m}^{-2}$) exposed to ambient CO_2 /control algal detritus, elevated CO_2 /control algal detritus and elevated CO_2 /algal detritus exposed to elevated CO_2 (white, light grey and dark grey bars, respectively)

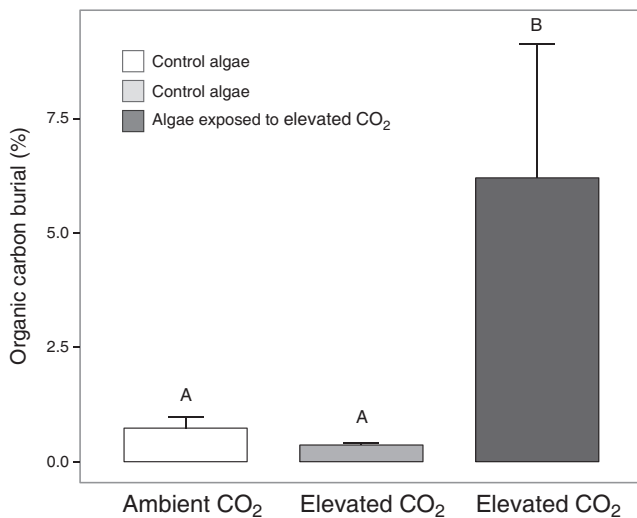
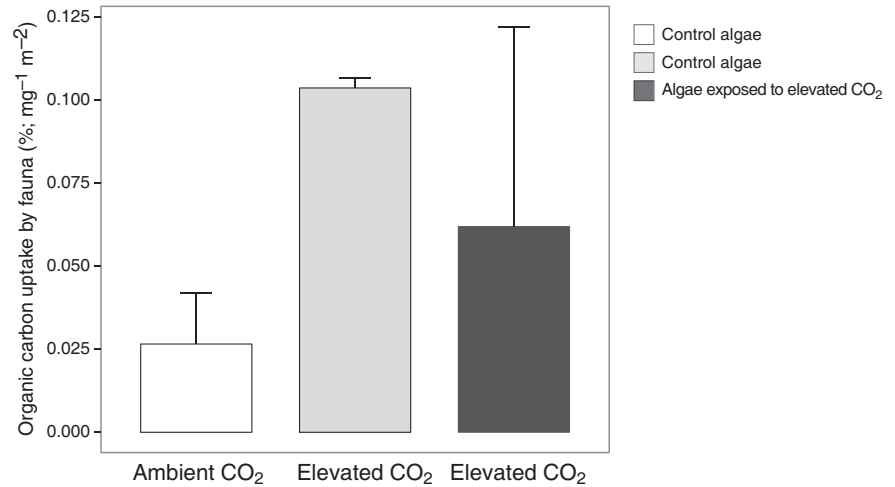


FIGURE 4 Organic carbon accumulation (mean \pm SE) in sediment (%; 2–6 cm layer) exposed to ambient CO_2 /control algal detritus, elevated CO_2 /control algal detritus and elevated CO_2 /algal detritus exposed to elevated CO_2 (white, light grey and dark grey bars, respectively)

There was no significant difference in carbon faunal uptake among different sources of algal detritus or between ambient and elevated CO_2 treatments (Table 1b; Figure 3). However, faunal uptake of control algal detritus tended to increase under elevated CO_2 levels (Figure 3).

Under enhanced CO_2 , sediment burial (layer 2–6 cm) of organic carbon from algal detritus previously exposed to elevated CO_2 was greater than that from algal detritus maintained at ambient CO_2 conditions (Table 1b; Figure 4). We found no accumulation of organic carbon in the 0–2 and 6–10 cm sediment layers for cores exposed to elevated CO_2 with algal detritus previously exposed to elevated CO_2 (Figure S2).

4 | DISCUSSION

Both elevated CO_2 and hypoxia significantly influenced the flux of organic carbon in marine sediments, as mediated by benthic biota. Infauna responded to elevated CO_2 by increasing the uptake of

algal detritus at normal O_2 concentrations, but not when exposed to hypoxia (Figure 5a,b). This suggests that metabolic depression may occur in marine invertebrates exposed to the combination of hypoxia and elevated CO_2 . As coastal areas with low O_2 and high CO_2 have increased globally and will continue to expand under future OA scenario, our results may suggest a limited ability of benthic communities to sustain normal mediation of important carbon cycling processes both under present and under future ocean conditions.

Ocean acidification can negatively affect benthic marine invertebrates, either directly, by altering physiological processes (Pan et al., 2015; Wang, Hu, Wu, Storch, & Poertner, 2018; Widdicombe & Spicer, 2008), or indirectly, via modification of food web interactions (Duarte et al., 2016; Kamyra et al., 2017; Queirós et al., 2015). Previous studies have shown that elevated CO_2 can result in reduced growth rate, disruption of extracellular acid–base balance, alteration of metabolism, lethargy and modification of individual level trade-offs in energy consuming processes of invertebrates, across different taxonomic groups (Kroeker, Kordas, Crim, & Singh, 2010; Portner & Farrell, 2008; Widdicombe & Spicer, 2008). Some species are able to maintain normal level of physiological activity under elevated CO_2 , although increasing metabolic rates and, thus, oxygen consumption (Pan et al., 2015; Queirós et al., 2015; Stumpp et al., 2012; Widdicombe & Spicer, 2008; Wood et al., 2008). For instance, Wood et al. (2008) found increased respiration and calcification rates and decreased arm muscle mass of the brittle star *Amphiura filiformis* under elevated CO_2 , indicating a trade-off between the maintenance of skeletal integrity and locomotion. Other studies have reported positive effects on the physiology (e.g. growth, calcification and metabolic rate) of molluscan species exposed to elevated CO_2 when resources were abundant, suggesting that food availability can mediate the susceptibility of marine invertebrates to OA (Pansch, Schaub, Havenhand, & Wahl, 2014; Ramajo, Marba, et al., 2016; Thomsen et al., 2013). In our study, elevated CO_2 significantly increased the organic carbon uptake by fauna at normoxia, suggesting that infaunal invertebrates were able to compensate short-term negative effects of elevated CO_2 through enhanced food intake.

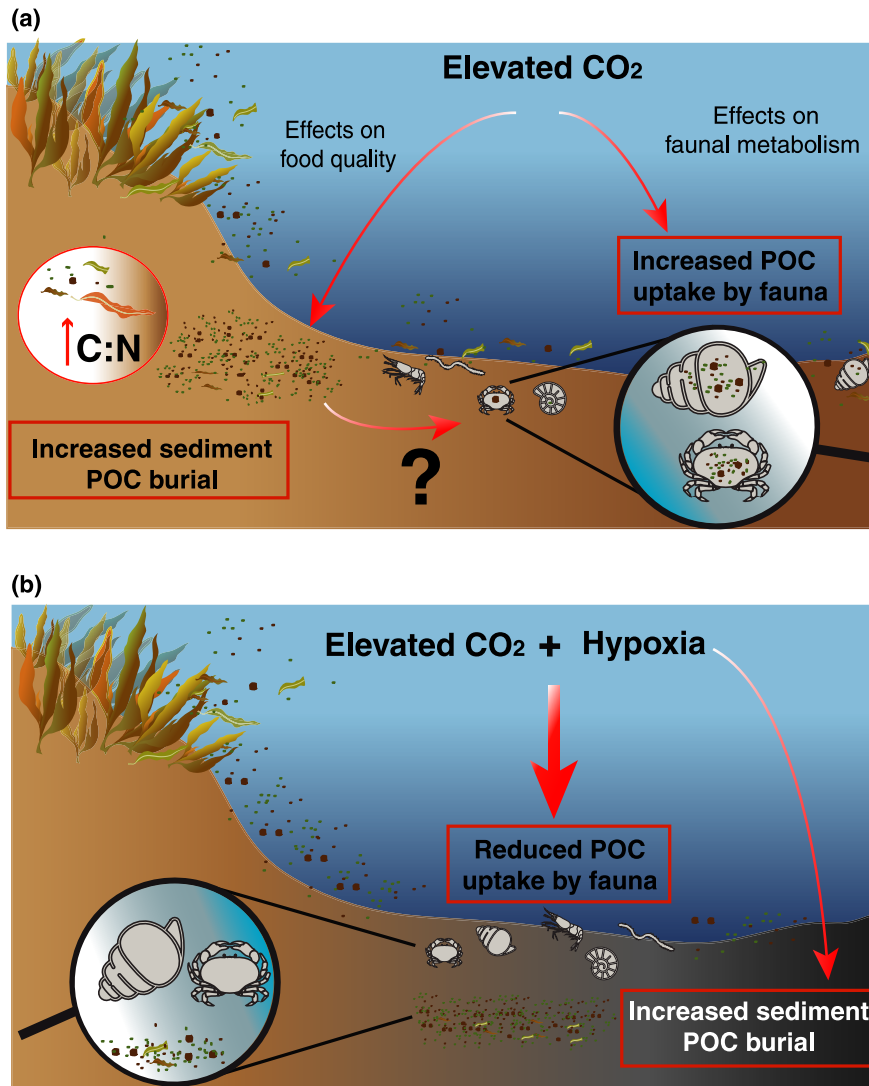


FIGURE 5 Schematic illustration showing the effects of elevated CO₂ and hypoxia on fauna-mediated particulate organic carbon (POC) fluxes in coastal seabed, based on results from the mesocosm experiment. (a) Increased POC uptake by fauna, when consumers were exposed to elevated CO₂ (direct effects of elevated CO₂ on faunal metabolism); enhanced POC burial in the sediment and high variability (question mark) in the POC uptake by fauna, when both consumers and resources (algal detritus) were exposed to elevated CO₂. (b) Hypoxia hindered the POC uptake by fauna at elevated CO₂ and increased the POC burial in the sediment, when consumers were exposed to the combined effects of elevated CO₂ and low oxygen

Elevated CO₂ can additionally affect the relationship between consumers and resources indirectly, by changing the nutritional quality of food (Duarte et al., 2016; Falkenberg, Russell, & Connell, 2013; Kamyra et al., 2017; Stiling & Cornelissen, 2007). We tested for this relationship and found that, under elevated CO₂ condition, the uptake of fauna fed with algal detritus grown at elevated CO₂ (higher C:N ratio) was highly variable and did not differ from that of algae previously maintained at ambient CO₂ (Figure 5a). Consumers can respond to changes in food nutritional quality at enhanced CO₂ either by preferentially consuming algae with higher nutritional quality (Falkenberg et al., 2013; Kamyra et al., 2017) or by increasing consumption of less nutritional food (i.e. compensatory feeding; Cruz-Rivera & Hay, 2001; Duarte et al., 2011, 2014), resulting in a species-specific feeding behaviour of consumers (Tomas, Martinez-Crego, Hernan, & Santos, 2015). The lack of a clear response of infauna to altered resource quality could also be due to the slight, though significant, increase in algal C/N ratio (~13%) under short-term elevated CO₂ condition, compared to those recorded in longer term elevated CO₂ experiments in terrestrial systems (Stiling & Cornelissen, 2007). The duration of our experiment (4 weeks) was

appropriate to detect the isotopic signal of traced carbon in primary consumers, whilst reducing changes in the measured response variables due to subsequent processing of labelled materials within the food web (Middelburg, 2014; Queirós et al., 2019). Further studies are, however, needed to evaluate how the persistence of elevated CO₂ conditions predicted under future climate scenarios can directly or indirectly modify resource-consumer relationships.

Importantly, once elevated CO₂ was applied with hypoxia, no increased carbon uptake by fauna was observed, suggesting limited capacity of marine invertebrates to cope with both stressors in combination. Feeding activity is a very oxygen demanding process and accounts for a large proportion of an organism's energy budget (Sokolova, 2013). Under hypoxia, the oxygen required by marine organisms to support energetically costly processes, such as feeding, assimilation and digestion of food, is not met by ambient oxygen supply. This means that also animals more tolerant to OA could be negatively affected by elevated CO₂ when concurrently exposed to hypoxia (Miller, Breitbart, Burrell, & Keppel, 2016; Portner, Langenbuch, & Michaelidis, 2005; Tomasetti, Morrell, Merlo, & Gobler, 2018). This suggests that in well-mixed shelf coastal systems,

as simulated in our study, even short-term hypoxic events may compromise the ability of marine invertebrates to deal with future ocean conditions. Indeed, benthic invertebrate contribution to sedimentary carbon cycling could be currently impaired in coastal areas exposed to low levels of oxygen and pH due to strong vertical stratification and high nutrient loading. Despite the predictions of an expansion of these hypoxic areas as a consequence of climate changes (Melzner et al., 2012), very few studies have, to date, investigated the cumulative effects of hypoxia and acidification on benthic communities (Gobler & Baumann, 2016). The combined effects of these stressors have been shown to reduce the survivorship and growth in bivalves (Gobler et al., 2014), reduce growth rate in abalone (Kim, Barry, & Micheli, 2013) and cause metabolic depression in different species of invertebrates, such as sipunculids, echinoderms and crustaceans (Portner et al., 2005; Steckbauer et al., 2015). Our results suggest that, in combination, elevated CO₂ and hypoxia may limit the ability of benthic communities to mediate globally important carbon fluxes on the seabed (Middelburg, 2018; Snelgrove et al., 2018).

Organic carbon accumulation was detected at the intermediate layer of sediment (2–6 cm), whilst we found no accumulation of carbon in the shallower and deeper sediment layers, regardless of experimental conditions. Organic matter arriving at the sediment surface may be subjected to many different processes. For instance, the organic carbon ingested by fauna may be egested back to the sediment and transferred through the food web or accumulated into deeper layers of the sediment. The carbon uptake by fauna and bacteria seems to be strongly related to their biomass (Woulds et al., 2016). In addition, at any trophic levels, organic carbon can be metabolized and remineralized through fast degradation (Gontikaki, van Oevelen, Soetaert, & Witte, 2011; Woulds et al., 2009). In our experiment, algal detritus added to the surface sediment was assimilated by fauna, which is particularly abundant in the top 0–2 cm layer, and then transferred to the underlying sediment layer (2–6 cm). The detection of carbon accumulation further away from the sediment–water interface may also be due to the lower abundance of animals found in the deeper part of sediment cores, thereby the remaining carbon was not consumed by animals and remained in the sediment. This result highlights the importance of faunal mediation towards carbon cycling, with mixing between sedimentary carbon pools and the overlying water reduced to those layers where fauna were more abundant.

We report here that hypoxia tended to increase organic carbon burial in the 2–6 cm layer, regardless of CO₂ concentration (Figure 5b), possibly as a consequence of alterations on infaunal assemblage functioning (Keil, 2017). Previous experimental studies, using carbon-labelled phytodetritus as a tracer, have shown that, under normoxia, both animals and microbes can assimilate labile carbon directly and respiration is generally the major fate of added labelled carbon (Woulds et al., 2016). Hypoxia may cause metabolic depression, reduced activity or lethargy in marine invertebrates (Galic, Hawkins, & Forbes, 2019; Levin et al., 2009), thereby indirectly promoting the organic carbon preservation in marine sediments. For instance, Jessen et al. (2017) have recently shown that

low oxygen negatively affected faunal diversity and activity (i.e. bioturbation) and promoted microbial anaerobic processes, resulting in a significant increase of the sediment organic carbon burial. To date, however, most studies estimating carbon fluxes on the seabed are still largely focused on physical and biogeochemical processes (Middelburg, 2018; Snelgrove et al., 2018). As recently highlighted in Queirós et al. (2019), continuing to ignore the vital mediation of seabed carbon cycling by invertebrates may likely limit our understanding of how the global ocean carbon cycle occurs, what processes and ecosystem components are involved, and what is their resilience under a changing ocean climate.

Elevated CO₂ concentration in seawater did not affect organic carbon burial in our experiment directly. The effects of elevated CO₂ on carbon sequestration in marine sediments are still unclear. Some laboratory studies have found an increase in microbial degradation of organic matter under elevated CO₂ that could lead to lower carbon sequestration under elevated CO₂ (Grossart et al., 2006; Piontek et al., 2013). However, the concurrent increase of primary production under elevated CO₂ could reduce microbial degradation of organic matter, resulting in negligible effects of OA on organic carbon burial. For instance, in a recent study, Zark et al. (2015) found no effects of elevated CO₂ on the concentration and molecular composition of organic carbon, despite a clear effect of phytoplankton on organic matter production, suggesting no change in the amount of organic matter in coastal systems under elevated CO₂ condition. In contrast, in our study, elevated CO₂ significantly increased the sediment deposition of algal detritus previously exposed to elevated CO₂, likely as a consequence of its decreased nutritional value (i.e. higher C:N ratio, Figure 5a). This is in accordance with previous work (Riebesell et al., 2007), where an increase in C:N ratio of primary producer tissues (about 16% at 700 µatm CO₂ level) was also observed under elevated CO₂, due to an overconsumption of dissolved inorganic carbon, leading to an increase in the export of particulate organic carbon. Stoichiometric changes of exported organic matter at elevated CO₂ could have a major impact on biogeochemical cycles (Figure 6; Andrews, Buitenhuis, Quéré, & Suntharalingam, 2017; Hofmann & Schellnhuber, 2009). Most of the oxygen consumed during organic matter respiration is used to oxidize carbon rather than nitrogen, thus resulting in excess oxygen consumption in deep water (Oschlies, Schulz, Riebesell, & Schmittner, 2008). In addition, elevated CO₂ may limit the sinking speed and transport of organic matter through the water column, by reducing the production of calcareous (CaCO₃) and siliceous (SiO₂) minerals, which provide ballast for the transport of organic carbon in deep water (Hofmann & Schellnhuber, 2009). This could, ultimately, result in shallower organic matter remineralization and further expansions of O₂ depletion zones (Andrews et al., 2017; Hofmann & Schellnhuber, 2009). Importantly, the combined effects of elevated CO₂ and hypoxia may slow down the mineralization of organic matter, likely increasing the burial of enhanced organic carbon production in marine sediments. Expansion of oxygen-depleted zones may increase denitrification and loss of fixed nitrogen, potentially impact nitrogen cycling and ocean productivity (Kalvelage et al., 2013). Our results highlight how

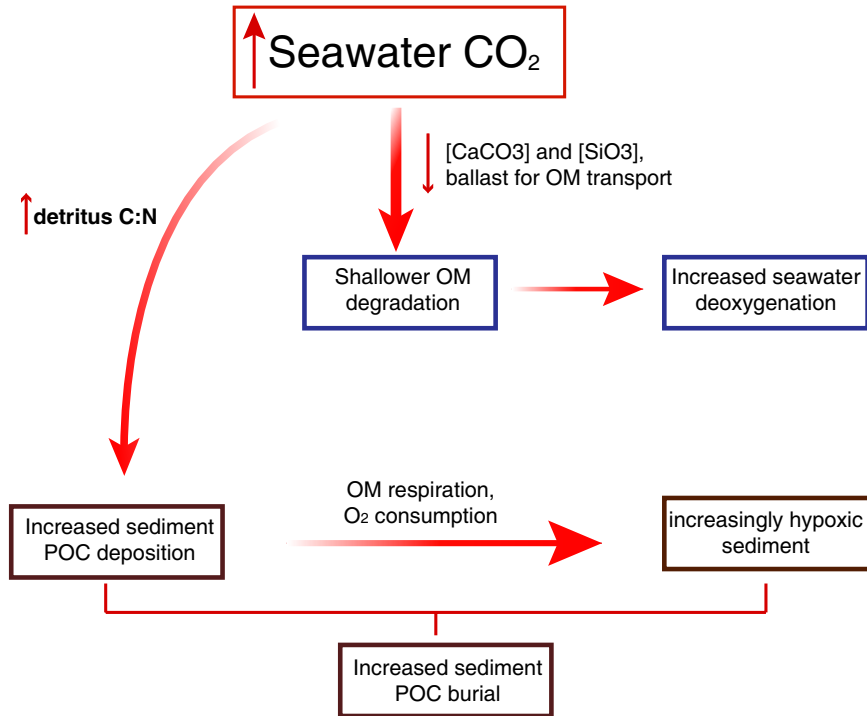


FIGURE 6 Diagram showing the potential impacts of elevated seawater CO₂ on biogeochemical cycles, either by changing the stoichiometric ratio of organic detritus, which arrives to the seabed, or reducing organic matter (OM) transport through the water column. Blue frames indicate processes in the water column; brown frames indicate processes at the seabed

changes in resources, in addition to consumers, may affect important processes determining ocean carbon cycling, and that food web interactions are key to predict ecosystem-level impacts of climate change.

In summary, the results of our experiment show that elevated CO₂ and episodic hypoxic events may affect net sequestration of organic carbon in coastal systems through the modification of relevant faunal-mediated pathways and resource quality. To the best of our knowledge, this is the first study experimentally investigating the combined effects of these two stressors on faunal-mediated carbon fluxes on a well-mixed coastal seabed. Episodic events of hypoxia, as simulated in our study, have been commonly documented in coastal systems, following intense depositions of organic matter at the seabed (Tait et al., 2015; Zhang et al., 2015). However, it is noteworthy that the persistence of low O₂ may also be driven by other seasonal and interannual cycles, depending on different processes, such as hydrodynamic conditions of the water body, thermal stratification and nutrient loads (Breitburg et al., 2018). Hypoxic areas, such as the Western Baltic Sea, the coasts of Japan and China or the Gulf of Mexico, are currently affected by coastal acidification, due to heterotrophic degradation of organic matter (Melzner et al., 2012; Thomsen et al., 2013). Thus, evaluating the combined effects of hypoxia and elevated CO₂ on marine life is essential for understanding how marine ecosystems respond to these conditions under both current and future climate conditions. In addition, further studies could also evaluate the impacts of future OA scenario on biological and biogeochemical processes in these coastal hypoxic systems already exposed to low O₂ and high CO₂ conditions. The capacity of marine organisms to sustain physiological processes under stress (e.g. reproduction, growth, calcification,

locomotion) may determine their survival under a changing climate (Widdicombe & Spicer, 2008). Increase of food uptake is a strategy that has been observed across taxa, and reflects higher metabolic costs to the individual associated with stress response pathways (Queirós et al., 2015; Thomsen et al., 2013). Our results indicated that this compensatory mechanism may be impaired under hypoxia, possibly weakening the ability of marine invertebrates to cope with elevated CO₂ and potentially reflects that higher metabolic costs will come at the expense of increased O₂ uptake rates in aerobes. Alternatively, a decrease in feeding rates could also represent a mechanism for marine organisms to deal with the exposure to elevated CO₂ and low O₂, by reducing aerobic metabolism and thus O₂ requirement (i.e. metabolic depression; Pörtner, Langenbuch, & Reipschläger, 2004; Rosa & Seibel, 2008). This could result in reduced growth rates and altered behaviour (Galic et al., 2019; Gobler et al., 2014; Tomasetti et al., 2018). Thus, hypoxia and elevated CO₂, in combination, may impair the key role of infaunal assemblages in determining carbon fluxes at the sediment–water interface and their contribution towards carbon sequestration (Queirós et al., 2019). In addition, changes in organic matter quality due to elevated CO₂ could increase the export of organic carbon in marine sediments and the expansion of low O₂ concentration, ultimately altering ecosystem functioning, including nitrogen cycling and ocean productivity at global scales (Hofmann & Schellnhuber, 2009; Kalvelage et al., 2013; Levin, 2018).

In this light, management actions aimed to reduce local stressors (e.g. eutrophication-driven hypoxia and coastal acidification) can be considered a good strategy for mitigating the impacts of global climate change (e.g. OA) on marine community functions and biogeochemical processes. For instance, although measures

to reduce eutrophication can take a long time to become effective (Varjopuro et al., 2014), increases in seawater oxygen concentration have been documented in some coastal systems, following nutrient input reduction (Kemp, Testa, Conley, Gilbert, & Hagy, 2009). As the incidence of hypoxia and elevated CO₂ are predicted to increase as a consequence of climate change (Breitburg et al., 2018; Gobler & Baumann, 2016), more studies are necessary to raise awareness of the impacts of multiple stressors on carbon fluxes in coastal marine sediments under future climate change scenarios, as well as to tune up suitable remediation strategies.

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