



## Organic matter processing in a [simulated] offshore wind farm ecosystem in current and future climate and aquaculture scenarios



H.E.E. Voet<sup>a,b,1</sup>, E. Vlamincx<sup>b,1</sup>, C. Van Colen<sup>b</sup>, S. Bodé<sup>c</sup>, P. Boeckx<sup>c</sup>, S. Degraer<sup>a,b</sup>, T. Moens<sup>b</sup>, J. Vanaverbeke<sup>a,b,\*</sup>, U. Braeckman<sup>b</sup>

<sup>a</sup> Royal Belgian Institute of Natural Sciences, Operational Directorate Natural Environment, Marine Ecology and Management, Vautierstraat 29, Brussels 1000, Belgium

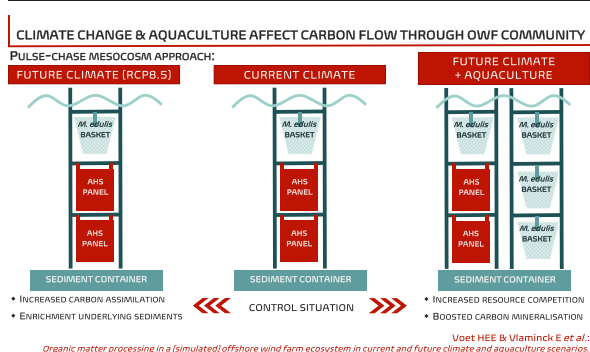
<sup>b</sup> Marine Biology Research Group, Department of Biology, Ghent University, Krijgslaan 281/S8, Ghent 9000, Belgium

<sup>c</sup> Isotope Bioscience laboratory – ISOFYS, Department of green Chemistry and Technology, Ghent University, Coupure links 653, Ghent 9000, Belgium

### HIGHLIGHTS

- Carbon assimilation by macrofauna species significantly boosted by climate change.
- Blue mussel (*M. edulis*) has dynamic (non-)trophic role in offshore wind farm community.
- Climate change has ecosystem-wide effects, including organic enrichment of sediment.
- Bivalve aquaculture induces higher inter- and intraspecific competition.

### GRAPHICAL ABSTRACT



### ARTICLE INFO

Editor: Daniel Wunderlin

#### Keywords:

Climate change  
Carbon assimilation  
Offshore wind farm  
Aquaculture  
Mesocosm experiment

### ABSTRACT

The rapid development of blue economy and human use of offshore space triggered the concept of co-location of marine activities and is causing diverse local pressures on the environment. These pressures add to, and interact with, global challenges such as ocean acidification and warming. This study investigates the combined pressures of climate change and the planned co-location of offshore wind farm (OWF) and aquaculture zones on the carbon flow through epifaunal communities inhabiting wind turbines in the North Sea. A <sup>13</sup>C-labelled phytoplankton pulse-chase experiment was performed in mesocosms (4 m<sup>3</sup>) holding undisturbed hard-substrate (HS) communities, natural sediment with infauna, and mobile invertebrate predators. Carbon assimilation was quantified under current and predicted future-climate conditions (+3 °C and −0.3 pH units), as well as a future-climate co-use scenario with blue mussel (*Mytilus edulis*) aquaculture. Climate change induced an increase in macrofaunal carbon assimilation as well as an organic enrichment of underlying sediments. Dynamic (non-)trophic links between *M. edulis* and other HS epifauna resulted in shifts among the species contributing most to the phytoplankton-derived carbon flow across climate scenarios. Increased inter- and intraspecific resource competition in the presence of *M. edulis* aquaculture prevented a large increase in the total assimilation of phytoplankton by HS fauna. Lower individual carbon assimilation rates by both mussels and other epifauna suggest that if filter capacity by HS epifauna would approach renewal by advection/mixing, *M. edulis* individuals would likely grow to a smaller-than-desired commercial size. In the same scenario, benthic organic carbon mineralisation was significantly boosted due to increased organic matter deposition by the aquaculture set-up. Combining these results with *in situ* OWF abundance data confirmed *M. edulis* as the most impactful

\* Corresponding author at: Royal Belgian Institute of Natural Sciences, Operational Directorate Natural Environment, Marine Ecology and Management, Vautierstraat 29, Brussels 1000, Belgium.  
E-mail address: [jvanaverbeke@naturalsciences.be](mailto:jvanaverbeke@naturalsciences.be) (J. Vanaverbeke).

<sup>1</sup> Joint first authorship.

OWF AHS species in terms of (total) carbon assimilation as well as the described stress responses due to climate change and the addition of bivalve aquaculture.

## 1. Introduction

Marine ecosystems are progressively being challenged on a local and global scale. In 2020, the global cumulative offshore wind power capacity reached 35.3GW and over 70GW is expected to be added worldwide by 2025 (GWEC, 2021). As the current global market leader in offshore wind farms (OWFs), Europe currently houses over 5400 offshore wind turbines (WindEurope, 2021). As such, a great quantity of artificial hard substrate (AHS) has been introduced into the otherwise mainly sandy environment of the North Sea. These new habitats are rapidly colonised by suspension feeders and, over time, develop into artificial reefs with diverse ecological structure and functioning (Degraer et al., 2020; Mavraki et al., 2020b). As part of the rapid development and diversification of the blue economy (the exploitation of marine and coastal resources), this has led to competition for offshore space and the progressive application of a multi-use approach in marine spatial planning (Schupp et al., 2019; MSP, 2020). The ‘multifunctional co-use’ of space and infrastructure between OWFs and mussel aquaculture is therefore increasingly being advocated as a favourable and profitable way forward (Steins et al., 2021), potentially adding to a local but strong functional shift towards a mainly suspension feeding OWF community.

On top of the local effects of offshore activities and infrastructure, climate change is challenging the marine environment on a global scale. Human activities have increased global carbon atmospheric dioxide (CO<sub>2</sub>) concentrations since the industrial revolution and have continued to increase them with about 20 ppm per decade since 2000, up to 10 times faster than any sustained rise in atmospheric CO<sub>2</sub> concentration during the past 800,000 years (Lüthi et al., 2008; Bereiter et al., 2015; IPCC, 2021). The ocean plays a crucial role in mitigating this anthropogenic CO<sub>2</sub> increase, but absorbing increasing amounts of CO<sub>2</sub> eventually leads to ocean acidification and alterations in the ocean carbon chemistry (Bindoff et al., 2019). A global average decrease of approximately 0.1 pH units in ocean surface waters has been observed since the start of the industrial revolution and this decline is predicted to reach a total decrease of 0.29 pH units towards the end of this century (Bindoff et al., 2019; IPCC, 2021). Furthermore, acidification rates in coastal environments can be up to an order of magnitude higher compared to those measured in open ocean systems (Provoost et al., 2010; Strong et al., 2014; Bindoff et al., 2019). Additionally, ocean warming is pressuring the marine environment with a predicted global mean sea surface temperature rise of approx. 3 °C by 2100 (Bindoff et al., 2019; IPCC, 2021).

These local and global changes can influence coastal ecosystems on different levels and in different ways. On a local scale, the introduction of AHS suspension feeding colonising fauna could eventually lead to bottom-up food web alterations through the reduction of the phytoplankton and micro- and meso-zooplankton biomass (Maar et al., 2007; Slavik et al., 2019) as well as an increased food availability for benthic-pelagic fish (Reubens et al., 2013; Mavraki et al., 2021). Wind turbines also affect hydrological conditions such as currents, stratification and sediment type, which in turn modify the benthic habitat (Braeckman et al., 2020). Additionally, the dense community of AHS colonising fauna on the turbine foundations increases the deposition of organic matter particles to the seafloor (Ivanov et al., 2021). Finally, all these processes affect the organic matter content and grain size distribution of the surrounding sediment habitat, referred to as ‘enrichment’ and ‘sediment fining’, respectively (Lefaille et al., 2018; Braeckman et al., 2020). Both are important factors for the diversity and species composition of the benthic community (Coates et al., 2014; Maar et al., 2009; Breine et al., 2018) and may affect benthic biogeochemical processes (De Borger et al., 2021).

Hence, the introduction of bivalve aquaculture in an offshore wind farm environment can affect the local ecosystem, both on a trophic and non-trophic scale. Introducing a large biomass of farmed filter feeding organisms may deplete local plankton concentrations and could affect the ecosystem's secondary production and the variety of higher trophic-level organisms preying upon those bivalves (Banas et al., 2007; Žydelis et al., 2009; Faulkner, 2013). On top of those trophic effects, bivalve aquaculture may also alter epifaunal community composition, e.g. through its artificial reef effect (Dumbauld et al., 2009; Cabre et al., 2021), and benthic community composition, e.g. through increased biodeposition (Gallardi, 2014; Cabre et al., 2021). The latter, redirecting organic matter towards the sediment, may also have cascading effects on biogeochemical cycling (Slavik et al., 2019; De Borger et al., 2021). Additionally, through their interaction with local hydrodynamics and their effect on nutrient and seston concentrations, large offshore aquaculture installations can affect the system's carrying capacity and, in turn, its potential to provide ecosystem services (Cabre et al., 2021).

Ocean acidification and warming are the main global stressors acting on the OWF AHS ecosystems. The ingestion of acidified water may cause physiological stress in all marine organisms (Pörtner et al., 2004) and disrupt their energy distribution and calcification regulation (Sokolova et al., 2012; Thomsen et al., 2015). Behavioural change and elevated food ingestion are typical adjustments observed in marine organisms coping with these stressors (Fabry et al., 2008; Dupont and Pörtner, 2013; Nagelkerken and Munday, 2016). Moreover, in highly abundant species, such increased feeding rates could significantly alter food source availability, possibly resulting in competition changes (Ong et al., 2017; Voet et al., 2021) and increased predation pressure (Rosenblatt and Schmitz, 2016).

The impact of both local and global stressors on coastal ecosystems can be profound and have been widely studied (e.g. Schupp et al., 2019; Steins et al., 2021; Degraer et al., 2021). These stressors will, however, occur simultaneously in a future offshore environment. Studies combining the interaction between both local (introduction and co-location of human activities) and global (climate change) levels of environmental pressures, are still largely missing.

Therefore, we experimentally tested the combined effect of climate change and aquaculture on the feeding ecology of the OWF colonising community. A mesocosm pulse-chase study was performed in which <sup>13</sup>C-labelled microalgae were offered to these OWF colonising communities. We hypothesised (1) a significant difference in carbon assimilation between OWF AHS colonising species, (2) an increase in OWF AHS macrofauna carbon assimilation in future climate conditions due to a stress-induced increase in feeding rate, (3) a reduction in macrofauna carbon assimilation in the CC + AQ mesocosm due to increased resource competition in the presence of blue mussel (*Mytilus edulis*) aquaculture and (4) an increase in benthic organic carbon mineralisation in the CC + AQ mesocosm as a result of increased organic matter deposition.

## 2. Methodology

### 2.1. Organism and sediment collection

In September 2018, hard substrate colonising fauna, natural sediment (with infauna) and mobile predators were collected on or near the C-Power OWF on the Thornton Bank, approximately 30 km off the Belgian coast.

The sampled hard substrate colonising fauna consisted of *Mytilus edulis*, carefully scraped from the D6 turbine in the C-Power OWF (51°33.04'N–02°55.42'E), and colonised PVC panels (15 × 15 cm) harvested from an ‘Artificial Hard Substrate Garden’ (ASHG). This AHS was developed to

facilitate the collection of artificial hard substrate (AHS) colonising organisms. The recovered plates were deployed in February 2018 by anchoring a bottom (1.5–2 m above seafloor) and mid-water (10–15 m above seafloor) mooring 6 km North-East of turbine D6 in C-Power OWF (51° 34.80'N–2° 59.76'E). The PVC panels were recovered by scientific divers in the first week of September 2018 and carefully packed in separate sealed plastic bags before being taken up to the surface.

Natural *in situ* sediment and associated infauna were collected within 500 m of the C-Power OWF using multiple Van Veen grabs (surface area 0.1 m<sup>2</sup>). Sediment was transferred immediately into sediment containers (Ø 0.6 m × h 0.3 m) without sieving, preserving the whole sediment community. Each container held approximately 0.07 m<sup>3</sup> natural sediment.

Mobile predators (the starfish *Asterias rubens*, the sea urchin *Psammechinus miliaris* and the swimming crab *Liocarcinus holsatus*) were collected by bottom trawling in the proximity of the C-Power OWF and a selection was handpicked (Table 2).

All *M. edulis* individuals, colonised AHS panels, mobile predators and sediment communities were stored in aerated seawater and transported to the experimental facilities within 4 h.

## 2.2. Experimental mesocosm set-up

All *M. edulis* individuals, AHS panels and natural sediment were placed in three mesocosm systems, while the mobile predators were temporarily incubated in two separate aquaria to delay their introduction into the simulated AHS community and avoid an excessive predation pressure at the start of the experiment. These separate aquaria were manipulated according to the same control (CTRL) and climate change (CC) regime as the three mesocosm systems (see below). Each mesocosm system consisted of a large cylindrical holding tank (Ø 2.2 m × h 1.4 m) equipped with a temperature-controlled continuous flow-through mechanism with a total of ± 4000 L in circulation. Water column mixing and currents were created by using four separate inflow locations in each mesocosm. Predator incubation systems were similar, with two aquaria containing the organisms (0.6 × 1.0 × 1.4 m) and a ± 1000 L temperature-controlled continuous flow-through mechanism on each aquarium. Both the mesocosm and

predator incubation systems were aerated and filled with natural seawater at pre-set laboratory conditions, mimicking the seawater salinity, temperature and pH at the time of the experiment (34 PSU, 19 °C and pH = 7.96; LifeWatch Belgium, 2015). All systems were subjected to a 12:12 h light/dark regime, mimicking natural diurnal light variations at the sea surface.

The three mesocosms were used to mimic three different scenarios through the respective manipulation of seawater temperature, pH and the standing stock of *M. edulis*: a control environment (CTRL: current temperature and pH), a climate change environment (CC: elevated temperature and lowered pH) and a climate change with aquaculture environment (CC + AQ: climate change conditions with additional *M. edulis*). Each mesocosm contained four 'OWF systems' (Fig. 1), each mimicking a wind turbine foundation with vertical zonation of colonising fauna and a sediment community at the bottom. Each 'OWF system' consisted of four elements: a PVC ladder with (1) a gridded *M. edulis* basket at the top, (2) an *in situ* colonised AHS panel from the mid-water mooring in the middle, (3) an *in situ* colonised AHS panel from the bottom mooring at the bottom of the ladder and, underneath the ladder, (4) a sediment container with natural sediment communities. In the CC + AQ mesocosm, each 'OWF system' had an additional PVC ladder with three gridded *M. edulis* baskets alongside it, reflecting the increased abundance of mussels in this environment (Fig. 1 right). Across all mesocosms, each *M. edulis* basket contained approximately 40 individuals, mimicking the relative AHS community densities at the location of sampling.

After an initial acclimatisation period of two weeks under ambient conditions, seawater temperature and pH were manipulated stepwise over a period of six days (+1 °C and –0.1 pH unit in each step), resulting in seawater of +3 °C and –0.3 pH units (conform IPCC RCP 8.5 predictions) in both CC environments compared to the CTRL environment. These conditions were maintained for 46 days. Seawater temperature was regulated using Aqua Medic Titan 8000 professional units (mesocosm systems) or TECO TK2000 heaters (mobile predators) and pH was manipulated through the controlled bubbling of CO<sub>2</sub> in the incubation tanks. Using JUMO (mesocosm systems) or IKS (mobile predators) temperature sensors and glass pH electrodes, all temperature and pH data was monitored, logged and manipulated automatically using a personalised Fleuren&Nooijen JUMO

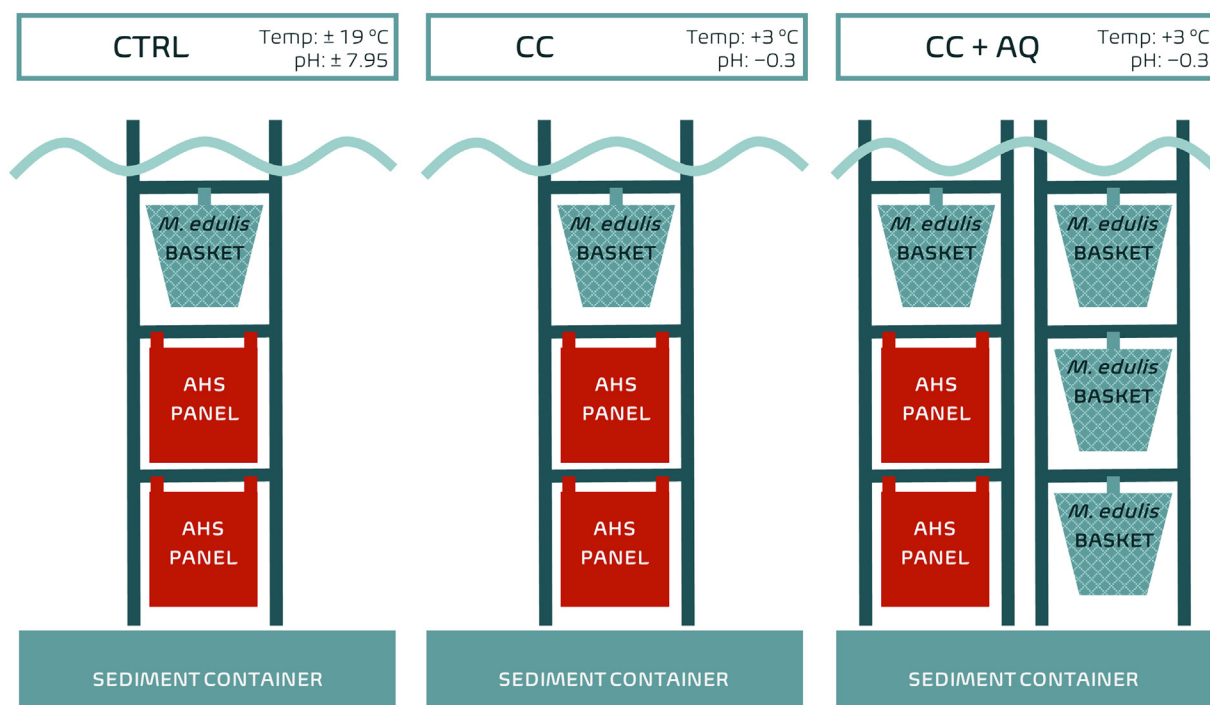


Fig. 1. Schematic overview of an 'OWF system' (4 in each mesocosm) with a *M. edulis* basket, an AHS panel from the mid-water (middle panel) and bottom mooring (bottom panel), and a sediment container in the CTRL and CC configuration (left and middle, respectively) and with 3 additional *M. edulis* baskets in the CC + AQ configuration (right).

microprocessor (mesocosm systems) or an IKS AquaStar aquaristic computer system (mobile predators).

Two-point calibration of the glass pH electrodes with Hanna Instruments™ NIST Reference Buffer Solutions (4.01 and 7.01) was performed weekly, as well as a back-up measurement of salinity, seawater temperature and pH (YSI® 30 M salinity system and Metrohm® 914 pH/Conductometer). Total Alkalinity (TA) was determined weekly on filtered (GF/C filter) 250 mL seawater samples from each mesocosm using a flow through titration analysis system (CONTROS HydroFIA™TA, 4H-JENA engineering GmbH, Germany). Seawater carbonate chemistry parameters ( $\text{pH}_T$ ,  $\text{pCO}_2$ ,  $\text{HCO}_3^-$ ,  $\text{CO}_3^{2-}$ ,  $\Omega_c$  and  $\Omega_a$ ) were calculated using CO<sub>2</sub>SYs software (Pierrot et al., 2006), using the thermodynamic constants of Mehrbach et al. (1973).

All organisms were allowed to acclimatise to manipulated conditions for 34 days and were fed three times a week by adding 40 mL or 100 mL Shellfish Diet 1800® (Instant Algae® mix by Reed Mariculture Inc.) to the CTRL and CC or CC + AQ mesocosms, respectively, and by adding juvenile *M. edulis* individuals and  $\pm 20$  g Marine Mix (RUTO frozen fishfood®) to the mobile predator aquaria. During this acclimatisation period, two replicate closed core incubations were performed weekly to measure sediment community oxygen consumption (SCOC) at the water-sediment interface in each mesocosm as a proxy for total organic matter degradation by benthic (micro)organism activity. Sediment cores were closed airtight and overlying seawater was fully mixed, allowing a steady measurement of the decrease in dissolved oxygen. Seawater oxygen concentration was measured continuously using PyroScience™ robust optical oxygen probes with REDFLASH-technology connected to a PyroScience™ FireSting O<sub>2</sub> logger. Oxygen consumption was subsequently calculated using the regression slopes of the O<sub>2</sub> concentration over time.

The acclimatisation period was followed by a background sampling event (day 34) to establish a non-enriched reference dataset of <sup>13</sup>C abundances ( $a^{13}\text{C}$ ). This was done by sacrificing one 'OWF system' from each mesocosm (with accompanying aquaculture system in CC + AQ) and collecting, identifying and storing ( $-20^\circ\text{C}$ ) all organisms attached to or associated with it. Additionally, seawater and sediment were sampled in each mesocosm (both stored at  $-20^\circ\text{C}$ ) for further analysis. At this point (day 34), a <sup>13</sup>C labelled *Isochrysis galbana* stock (see below) was added to each mesocosm. Five days after the addition of the labelled algae (day 39), two complete 'OWF systems' were sacrificed from each mesocosm. Subsequently, the (manipulated) mobile predators were added to the mesocosms. The densities of these predators mimicked reported average natural OWF macrofauna community ( $10 \times A. rubens$ ,  $4 \times L. holsatus$  and  $8 \times P. miliaris$  per mesocosm; De Mesel et al., 2013; De Backer et al., 2020; Degraer et al., 2020). The delayed introduction of mobile predators was chosen to allow sufficient time for <sup>13</sup>C assimilation in the lower trophic levels before including the higher trophic levels in the mesocosm. The final 'OWF system' in each mesocosm was sampled 12 days after the addition of the labelled algae (day 46).

### 2.3. Labelled algae

The microalga *Isochrysis galbana* was reared from a subsampled MarBiol (UGent) stock and cultured at  $23^\circ\text{C}$  under continuous light in autoclaved seawater supplemented with NutriBloom medium (PhytoBloom) and 10 g Sodium bicarbonate (99 % <sup>13</sup>C) per 60 L *I. galbana* stock. Subsequently, the microalga culture was allowed to grow until even distribution across the three mesocosms would create the desired algal density of  $\pm 145$  mg C m<sup>-3</sup> in each mesocosm, mimicking the annual mean phytoplankton biomass close to the Thornton Bank (Baretta-Bekker et al., 2009). The labelled microalgae had reached a <sup>13</sup>C abundance ( $a^{13}\text{C} = \text{<sup>13</sup>C/C}$ ) of  $5.85 \pm 1.93$  % ( $a^{13}\text{C} \pm \text{SD}$ ) when added to the experimental mesocosms.

### 2.4. Laboratory analysis

Before stable isotope analysis, all 'OWF system' samples (including sediment and seawater filters) were oven-dried at  $60^\circ\text{C}$  for 48 h. Dried

organism and sediment samples were weighed and ground with a pestle and mortar until a fine homogenous powder was obtained. Subsequently, subsamples of  $\pm 100$   $\mu\text{g}$  organic carbon were weighed in silver or tin cups (5–8 mm, Elemental Microanalysis UK) for samples with or without a calcareous fraction, respectively. After the addition of 10  $\mu\text{L}$  milli-Q® water, the silver cups were placed in a glass desiccator with HCl vapour ( $\pm 50$  mL 37 % HCl) for 24 h to remove the calcareous fragments' carbon (modified from Harris et al., 2001). Subsequently, all subsamples were oven-dried at  $60^\circ\text{C}$  for 24 h.

Ground organisms were standardly encapsulated individually, or multiple individuals of the same species sampled in the same mesocosm at the same time were pooled together (if available) when individual mass was not sufficient. Stable Isotope Analysis (SIA) was performed at the Isotope Bioscience Laboratory (ISOFYS, Ghent University, Belgium). Carbon isotopic composition was analysed using an ANCA-GSL elemental analyser interfaced with a 20–22 Isotope Ratio Mass Spectrometer (SerCon, Cheshire, UK). Isotopic samples were measured relative to laboratory standards (adjusted to sample size) and a quality analysis (QA) sample was run every ten samples (Sorghum EM-B2159). <sup>13</sup>C normalisation ( $\pm$  cumulative uncertainty on the scale) to Vienna Pee Dee Belemnite (VPDB) standard scale was done using WHEAT IA-R001 ( $\delta^{13}\text{C} = -26.43 \pm 0.08$  ‰ vs. VPDB, calibrated by Iso-analytical towards IAEA-CH6) and an in-house QA reference (Sorghum  $\delta^{13}\text{C} = -13.78 \pm 0.17$  ‰ vs. VPDB). Average analytical standard deviation on the  $\delta$  value was determined by measuring five replicates of a sample of Alanine ( $\delta^{13}\text{C} = -25.16 \pm 0.20$  ‰ vs. VPDB). For the enriched samples, the QA reference was a synthetically <sup>13</sup>C-enriched maize sample ( $\delta^{13}\text{C} = 396.9 \pm 0.37$  ‰ vs. VPDB).

### 2.5. Carbon assimilation

Isotopic composition is commonly expressed using the delta notation, i.e. the deviation of the carbon isotopic ratio (<sup>13</sup>C:<sup>12</sup>C) of a given sample (<sup>13</sup>R<sub>sample</sub>) relative to that of a scale reference. For <sup>13</sup>C, the scale reference is conventionally Vienna Pee Dee Belemnite standard (VPDB) with  $^{13}\text{R}_{\text{VPDB}} = 0.0111802$ , where

$$\delta^{13}\text{C} = \left[ \frac{^{13}\text{R}_{\text{sample}}}{^{13}\text{R}_{\text{VPDB}}} - 1 \right]$$

Carbon assimilation was calculated as

$$\text{Carbon assimilation} [C_{\text{assimilated}} C_{\text{biomass}}^{-1}] = \frac{a^{13}\text{C}_{\text{sample}} - a^{13}\text{C}_{\text{background}}}{a^{13}\text{C}_{\text{labelled algae}} - a^{13}\text{C}_{\text{natural algae}}}$$

with  $a^{13}\text{C}_{\text{sample}}$ ,  $a^{13}\text{C}_{\text{background}}$ ,  $a^{13}\text{C}_{\text{labelled algae}}$ , and  $a^{13}\text{C}_{\text{natural algae}}$  the  $a^{13}\text{C}$  of the sample, 'natural' background sample, labelled algae and natural algae. The  $a^{13}\text{C}$  of natural *I. galbana* was obtained from Breteleur et al. (2002).

Individual carbon assimilation [ $\mu\text{gC ind}^{-1}$ ] was subsequently calculated by multiplying the carbon assimilation with the carbon content [C] of each sample to obtain the assimilation per biomass, and further multiplying this by the species-specific mean biomass of an individual. Such an individual carbon assimilation was calculated for each sample and subsequently averaged per species, per sampling event and per mesocosm.

To assess mesocosm carbon budgets, the mean individual carbon assimilation [ $\mu\text{gC ind}^{-1}$ ] of each macrofauna species was multiplied by the species' abundance to estimate the total carbon assimilation [ $\mu\text{gC}$ ] of each species in each mesocosm. The carbon uptake by the zooplankton community was not quantified, as no zooplankton was recovered in the mesocosm and was likely already consumed by the high amount of filter and suspension feeders present. Other sources and sinks, such as the organisms' respiration, dissolved (in)organic carbon (DIC/DOC) and carbon assimilated in dead organisms that did not fall and settle in the sediment containers below the 'OWF systems', were not quantified and consequently, the carbon budget in each mesocosm could not be closed completely.



## 2.6. Data analysis

Due to an unbalanced dataset and high kurtosis of the isotopic data, a non-parametric approach (Kruskal-Wallis Rank Sum test) was used to test for (1) differences in mean carbon assimilation between species within a mesocosm, (2) differences in mean carbon assimilation between experimental mesocosms within a species, and (3) differences in total carbon assimilation. Species with <3 replicates per sampling event or experimental mesocosm were excluded from the analyses. The Dunn's Kruskal-Wallis Multiple Comparisons test (KWMC) was used for post-hoc analysis of differences. The SCOC measured in each mesocosm was compared using one-way analysis of variance (ANOVA) and Tukey's Honest Significant Differences (HSD) post-hoc test. SCOC data was normally distributed and homogeneity of variances was checked using Levene's test. All statistical analyses were handled at the 5 % significance level and conducted using R Studio software version 1.4.1106 (RStudio Team, 2016).

## 3. Results

### 3.1. Mesocosm environments

Temperature ( $\pm$ SD) in the future climate mesocosms (CC and CC + AQ) was raised on average by  $3.02 \pm 0.17$  °C and  $3.08 \pm 0.17$  °C, respectively, compared to CTRL (Table 1; Appendix A). Seawater pH ( $\pm$ SD) was reduced on average by  $0.29 \pm 0.02$  in CC and  $0.30 \pm 0.02$  in CC + AQ, compared to CTRL (Table 1; Appendix A).

Although there were small differences in salinity between the mesocosms, these were well within the naturally occurring salinity range of the sampling site. The total alkalinity, as a measure for the seawater's buffering capacity, along with other carbonate chemistry parameters, stably differed between mesocosms according to the imposed climate manipulations (Table 1).

### 3.2. Macrofaunal abundance and biomass

A total of 18 macrofauna species were recovered in the mesocosms at the end of the experiment. These included both primary consumers and higher trophic levels (Table 2). After exclusion of species with less than three successfully analysed replicate samples in terms of isotopic composition (marked \* in Table 2), a total of 13 species was further analysed. Most species were found in all three mesocosms, apart from the nudibranch *Aeolidia filomenae*, which was missing in CC + AQ, the gastropod *Crepidula fornicata* missing in CC, and amphipods (*Jassa herdmani* and *Monocorophium acherusicum*) missing in CTRL. Additionally, three species of mobile predators (marked † in Table 2) were introduced 5 days after adding the labelled algae, meaning any individuals of these species found before this time or in excess of the added numbers, originated from the AHSg plates or from *in situ* sediment translocated to the mesocosms.

**Table 1**

Average seawater carbonate chemistry of three mesocosms [CTRL: control, CC: climate change and CC + AQ: climate change with aquaculture] throughout 46-day mesocosm experiments ( $\pm$ SD): temperature (°C), pH, salinity (PSU), Total Alkalinity (TA;  $\mu\text{mol kg}^{-1}$ ), partial pressure of CO<sub>2</sub> (pCO<sub>2</sub>;  $\mu\text{atm}$ ), total inorganic carbon concentration (C<sub>T</sub>;  $\mu\text{mol kg}^{-1}$ ), concentration of bicarbonate and carbonate ion (HCO<sub>3</sub><sup>-</sup> and CO<sub>3</sub><sup>2-</sup>;  $\mu\text{mol kg}^{-1}$ ) and saturation state of the seawater with respect to aragonite ( $\Omega_A$ ) and calcite ( $\Omega_C$ ).

	CTRL	CC	CC + AQ
Temperature (°C)	18.98 $\pm$ 0.05	22.03 $\pm$ 0.33	22.09 $\pm$ 0.04
pH	7.95 $\pm$ 0.01	7.66 $\pm$ 0.01	7.65 $\pm$ 0.00
Salinity (PSU)	33.03 $\pm$ 0.33	36.27 $\pm$ 0.33	34.74 $\pm$ 0.55
TA ( $\mu\text{mol kg}^{-1}$ )	1985 $\pm$ 13	2170 $\pm$ 38	1865 $\pm$ 85
pCO <sub>2</sub> ( $\mu\text{atm}$ )	442 $\pm$ 12	1028 $\pm$ 34	911 $\pm$ 31
C <sub>T</sub> ( $\mu\text{mol kg}^{-1}$ )	1808 $\pm$ 14	2067 $\pm$ 38	1778 $\pm$ 79
HCO <sub>3</sub> <sup>-</sup> ( $\mu\text{mol kg}^{-1}$ )	1668 $\pm$ 14	1946 $\pm$ 36	1677 $\pm$ 77
CO <sub>3</sub> <sup>2-</sup> ( $\mu\text{mol kg}^{-1}$ )	126 $\pm$ 3	90 $\pm$ 1	73 $\pm$ 5
$\Omega_A$	1.97 $\pm$ 0.04	1.39 $\pm$ 0.02	1.14 $\pm$ 0.07
$\Omega_C$	3.05 $\pm$ 0.06	2.12 $\pm$ 0.03	1.75 $\pm$ 0.11

**Table 2**

Abundance (n) of organisms recovered in each sampling event (5 or 12 days after addition of labelled algae) in each mesocosm: control [CTRL], climate change [CC] and climate change with aquaculture [CC + AQ]. Species with asterisk [\*] were excluded from analysis due to unsuccessful isotopic analysis or number of replicate subsamples <3; species with dagger (†) were added separately as 'mobile predators' (see Methodology) and the numbers of mobile predators added intentionally are indicated between brackets. Notice *A. rubens* and *P. miliaris* were found both on AHS panels and in the sediment.

	CTRL		CC		CC + AQ	
	5 days	12 days	5 days	12 days	5 days	12 days
<i>Abra alba</i> *	–	1	–	–	–	–
<i>Aeolidia filomenae</i>	1	–	1	–	–	–
<i>Amphiuira filiformis</i> *	–	–	–	–	1	–
<i>Asterias rubens</i> †	–	7 (10)	1	8 (10)	–	5 (10)
<i>Asterias rubens</i> in sediment	1	7	–	–	6	5
<i>Crangon crangon</i> *	–	–	–	1	1	–
<i>Crepidula fornicata</i>	3	–	–	–	–	1
<i>Eulalia viridis</i>	2	–	1	–	–	2
<i>Hediste diversicolor</i>	4	5	3	1	11	5
<i>Jassa herdmani</i>	–	–	5	53	38	26
<i>Leptoplana tremellaris</i>	13	–	5	20	–	11
<i>Liocarcinus holsatus</i> †	2	5 (4)	2	1 (4)	1	2 (4)
<i>Metridium senile</i>	2	3	4	7	12	5
<i>Monocorophium acherusicum</i>	–	–	119	–	48	–
<i>Mytilus edulis</i>	70	35	70	35	280	140
<i>Necora puber</i> *	–	–	–	1	–	–
<i>Ophiura ophiura</i> *	–	–	–	–	1	–
<i>Pisidia longicornis</i>	6	8	14	18	1	–
<i>Psammochinus miliaris</i> †	–	7 (8)	–	15 (8)	–	10 (8)
<i>Psammochinus miliaris</i> * in sediment	–	–	–	–	7	–

Abundance of blue mussels (*M. edulis*) was consistently high, with 420 and 105 individuals recovered in the mesocosms with (CC + AQ) and without (CTRL & CC) aquaculture, respectively. The second and third most abundant taxa were the amphipods *J. herdmani* and *M. acherusicum*, ranging between 0 and 119 individuals. The abundance of the remaining species ranged between 0 and 20 individuals per mesocosm. The total organic carbon biomass in the experiments was highest for (soft tissue of) *M. edulis* (30.94 gC in CC, 33.75 gC in CTRL and 133.96 gC in CC + AQ), followed by that of the swimming crab *L. holsatus* in CTRL (4.58 gC), *L. holsatus* and the sea urchin *P. miliaris* in CC + AQ (2.23 gC and 1.78 gC, respectively) and the starfish *A. rubens* in CC (0.73 gC). All other species in each mesocosm had a total organic carbon biomass <1 gC. The enriched  $\delta^{13}\text{C}$  signatures [‰ vs. VPDB] of 351 individual samples ranged between  $-18.7$  ‰ (for *M. edulis* in CC + AQ) and 518.3 ‰ (for *J. herdmani* in CC; Table 3).

### 3.3. Carbon assimilation

#### 3.3.1. Species-specific effects

Between-species comparisons within each mesocosm (Appendix B) revealed that the mean (biomass-specific) carbon assimilations ( $\pm$ SD; C assimilated per C biomass, reported here as %) measured in CTRL were highest in *C. fornicata* ( $8.73 \pm 0.19$  %), *Pisidia longicornis* ( $5.36 \pm 1.24$  %) and *M. edulis* ( $3.16 \pm 1.27$  %). All other species present in CTRL had a mean carbon assimilation below 2.00 %. In the CC mesocosm, a mean carbon assimilation above 2.00 % was measured in *P. longicornis* ( $7.67 \pm 2.65$  %), *J. herdmani* ( $7.05 \pm 3.89$  %), *M. acherusicum* ( $4.45 \pm 2.37$  %), *M. edulis* ( $3.60 \pm 2.24$  %) and *Leptoplana tremellaris* ( $3.00 \pm 0.96$  %). The CC + AQ mesocosm showed lower carbon assimilation levels overall, with *J. herdmani* ( $3.13 \pm 1.19$  %) being the only species with a carbon assimilation exceeding 2.00 %. Generally, the mean carbon assimilations of the 'winning' species in each mesocosm were significantly higher than that of the respective 'losers' (Appendix B).

#### 3.3.2. Climate change and aquaculture effects

Between-mesocosm comparison within each species (Fig. 2) revealed that (biomass-specific) carbon assimilation of *J. herdmani* and

**Table 3**  
Range of stable carbon isotopic signatures [ $\delta^{13}\text{C}$  in ‰ vs. VPDB] of all background and enriched samples, for all species included in analysis.

	Background		Ctrl		CC		CC + AQ	
	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.
<i>A. filomenae</i>	-18.3	-17.8	-17.2	-17.1	-	-	-	-
<i>A. rubens</i>	-19.6	-17.8	-14.8	258.1	14.7	26.5	3.6	20.9
<i>A. rubens</i> in sediment	-19.4	-17.3	35.5	44.5	7.6	16.2	-16.3	-9.0
<i>C. fornicata</i>	-25.8	-25.8	347.0	363.9	-	-	-	-
<i>E. viridis</i>	-19.1	-18.3	-14.7	-13.4	-	-	-	-
<i>H. diversicolor</i>	-17.0	-17.0	-14.7	25.6	-7.2	84.4	-17.8	-8.9
<i>J. herdmani</i>	-18.6	-15.3	-	-	38.1	518.3	66.7	176.1
<i>L. tremellaris</i>	-19.9	-18.8	63.7	67.6	71.5	150.5	38.3	39.6
<i>L. holsatus</i>	-18.7	-17.7	-18.4	96.8	-	-	-10.7	6.8
<i>M. senile</i>	-19.2	-16.0	-16.4	-2.0	12.2	91.9	-12.6	17.3
<i>M. acherusicum</i>	-18.8	-17.0	-	-	20.3	279.2	21.1	79.8
<i>M. edulis</i>	-21.5	-17.1	36.5	212.9	-2.1	317.1	-18.7	95.1
<i>P. longicornis</i>	-23.8	-18.1	132.5	290.7	150.9	446.9	-	-
<i>P. miliaris</i>	-24.1	-24.1	-13.0	28.5	-18.2	18.3	-13.9	8.4
Sediment	-23.1	-22.0	18.1	43.9	45.8	54.1	18.9	20.1
Water	-21.3	-21.3	57.8	58.2	88.3	192.5	19.9	28.0

*L. tremellaris* were significantly higher in CC compared to CC + AQ ( $p_{\text{adj}} = 0.032$  and  $p_{\text{adj}} = 0.010$ , respectively). Additionally, carbon assimilation of *M. senile* was significantly higher in CC compared to CTRL ( $p_{\text{adj}} = 0.004$ ) and CC + AQ ( $p_{\text{adj}} = 0.028$ ). Carbon assimilation in CC + AQ was significantly lower compared to CTRL for benthic *A. rubens* ( $p_{\text{adj}} = 0.008$ ) and *Hediste diversicolor* ( $p_{\text{adj}} = 0.017$ ). *M. edulis* also assimilated significantly less in CC + AQ compared to CTRL ( $p_{\text{adj}} = 0.001$ ) and CC ( $p_{\text{adj}} < 0.001$ ).

### 3.4. Mesocosm carbon budget

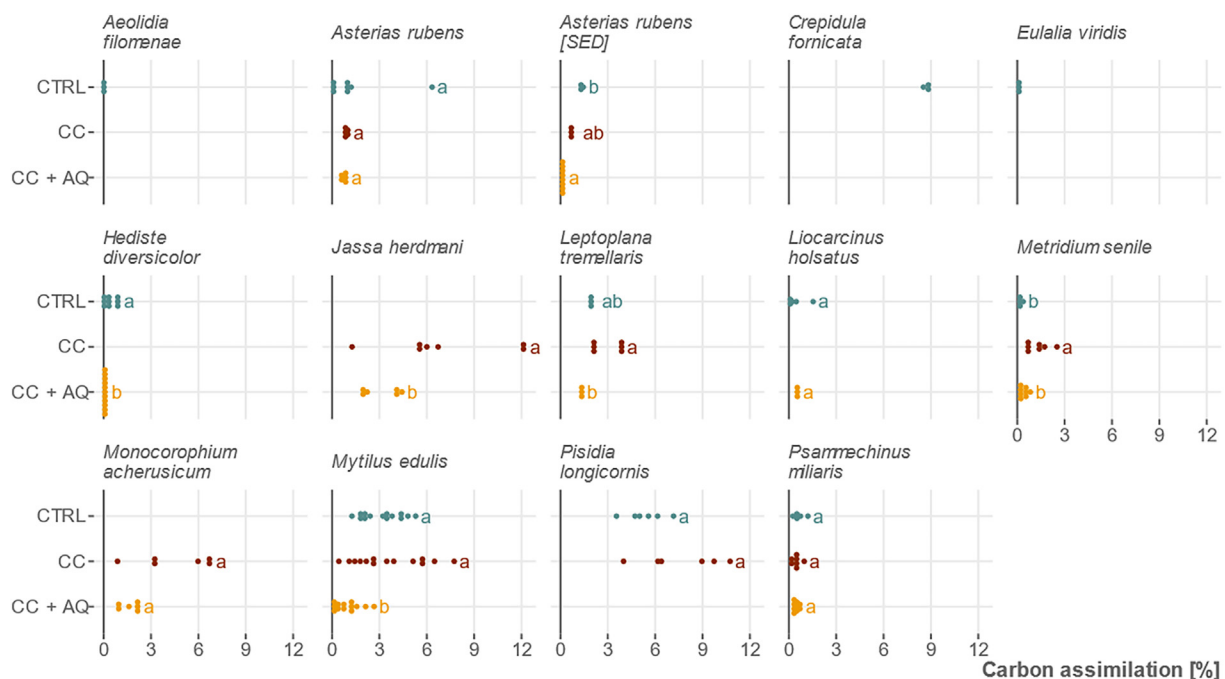
Of the total carbon added to each mesocosm as labelled algae, the OWF macrofauna community assimilated 25.0 % in CTRL, 26.5 % in CC and 29.1 % in CC + AQ. Another fraction of the total added microalgal carbon was recovered at the end of the experiment in the sediment and water present in the mesocosms. An estimated total of 7.3 % was recovered in

CTRL sediment and 0.9 % in CTRL water (Fig. 3). In the CC mesocosm, the corresponding values for sediment and water were 15.1 % and 2.8 %, respectively, while in the CC + AQ mesocosm, they were 7.1 % and 0.4 % (Fig. 3).

Altogether, 33.4 % of the total added microalgal carbon in CTRL could be allocated to either macrofauna carbon assimilation or the carbon fraction recovered in mesocosm sediment and water. In CC, 44.4 % of the total carbon budget could be allocated accordingly and in CC + AQ, this was 36.6 % (Fig. 3).

At the end of the experiment, *M. edulis* had assimilated the largest share of the added labelled algae carbon, significantly more than all other species combined in each mesocosm (Dunn's KWMC, all  $p_{\text{adj}} \leq 0.024$ ; Fig. 4), corresponding to 96.5 %, 96.8 % and 93.6 % of all assimilated carbon by macrofauna in CTRL, CC and CC + AQ, respectively. The 2nd and 3rd highest total carbon assimilation by macrofauna was found within a set of the same three species across the three mesocosms: *L. holsatus* (2.6 % in CTRL and 3.3 % in CC + AQ), *A. rubens* (0.5 % in CTRL and 2.0 % in CC) and *P. miliaris* (0.7 % in CC and 4.9 % in CC + AQ). These three species match the selection of mobile predators added intentionally on day 39 (see Methodology; Fig. 4).

A share of the remaining microalgal carbon budget was processed through respiration, partly by the colonising macrofauna and sediment community present in each 'OWF system' in the mesocosms. The mean sediment community oxygen consumption (SCOC), as an estimate of organic carbon mineralisation by the sediment community, differed significantly between mesocosms ( $F_{2,15} = 57.31$ ;  $p < 0.001$ ). The mean SCOC ( $\pm$ SD) in CC + AQ ( $45.41 \pm 6.38 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ ) was significantly higher than in CTRL ( $24.41 \pm 5.11 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ ; Tukey HSD,  $p_{\text{adj}} < 0.001$ ), which was, in turn, significantly higher than in CC ( $14.83 \pm 3.40 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ ;  $p_{\text{adj}} = 0.01$ ). When considering the total sediment surface area present in each mesocosm (including the removal of one 'OWF system' after 5 days) and assuming an aerobic respiration ratio ( $\text{O}_2:\text{C}$ ) of 1:1, these rates amassed to a mean estimated total ( $\pm$ SD) of  $1.81 \pm 0.57 \text{ gC}$ ,  $1.10 \pm 0.32 \text{ gC}$  and  $3.36 \pm 0.57 \text{ gC}$  remineralised by the sediment communities in CTRL, CC and CC + AQ, respectively, over the course of 12 days. Total Organic Carbon (TOC) of the sediment was determined at each of the three sampling events (i.e. background sampling, as well as 5 and 12 days after addition of labelled



**Fig. 2.** Carbon assimilation [ $C_{\text{assimilated}} C_{\text{biomass}}^{-1}$ , presented here in %] per species and per mesocosm. Letters represent compact letter display of significant differences between mesocosms within each species (Kruskal-Wallis Rank Sum test): mesocosms sharing a letter do not differ significantly after Bonferroni correction.

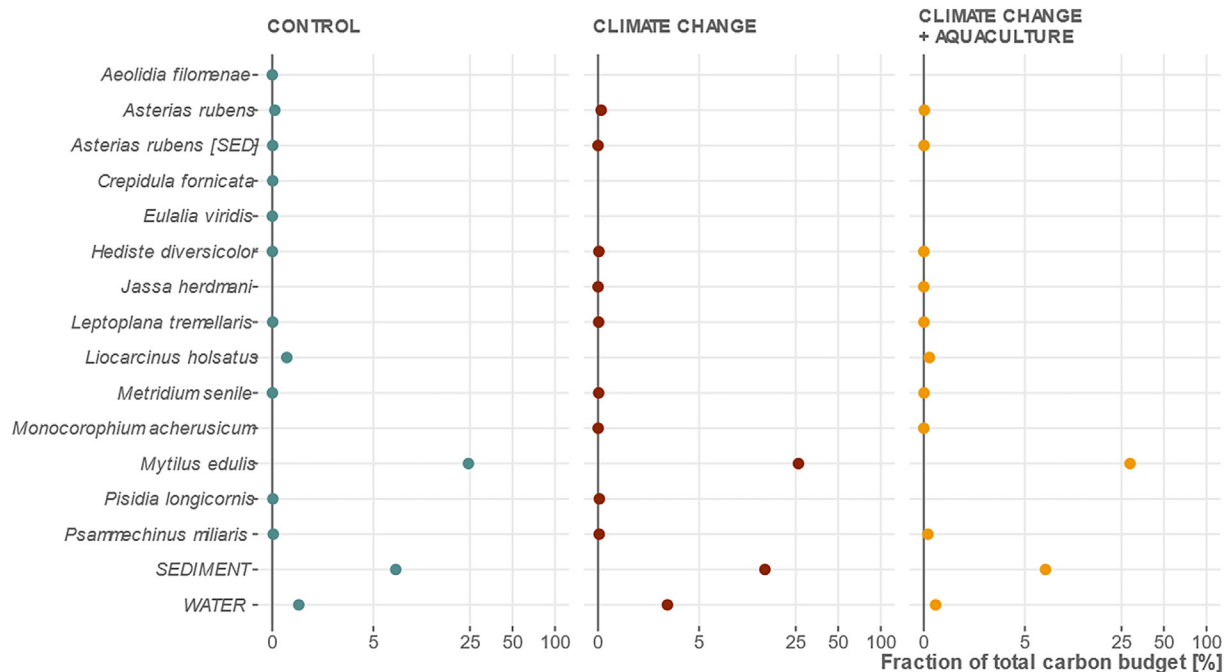


Fig. 3. Recovery of total added macroalgal carbon budget at the end of the experiment in all macrofauna species, sediment and water in each mesocosm on a logarithmic scale.

algae). In CTRL and CC + AQ, TOC remained similar throughout the experiment, ranging between 0.04 and 0.07 %. In CC, TOC seemingly increased towards the end of the experiment, as values ranged from 0.11 % at the start to 0.21 % at the end of the experiment.

4. Discussion

In this study, the carbon assimilation by the typical OWF colonising fauna and associated sediment community was experimentally quantified

under current and predicted future climate conditions, including a ‘multi-functional co-use’ scenario with blue mussel (*M. edulis*) aquaculture activities within the OWF area. The results confirmed our hypotheses: (1) carbon assimilation differed significantly between OWF species across different trophic levels, (2) climate change conditions significantly affected carbon assimilation of artificial hard substrate (AHS) colonising fauna, and (3) the presence of *M. edulis* aquaculture reduced overall carbon assimilation in a closed mesocosm OWF AHS system as well as (4) boosted sediment mineralisation rates.

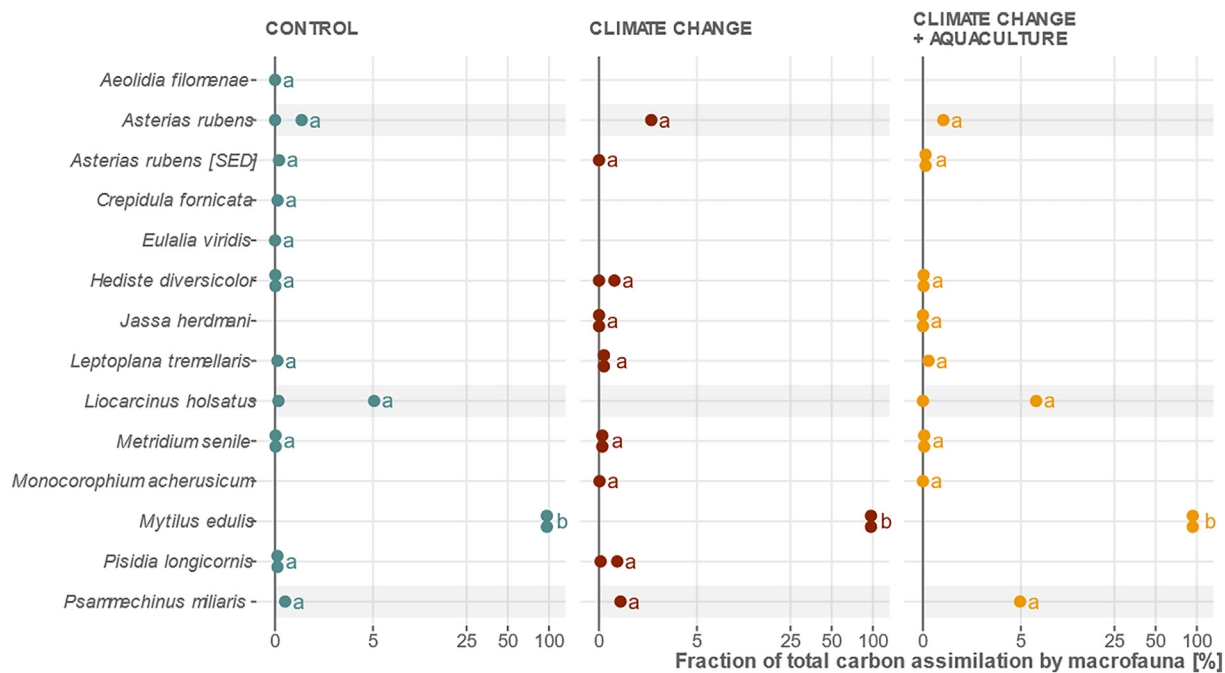


Fig. 4. Total carbon assimilation by macrofauna per species from both sampling events in each mesocosm on a logarithmic scale. Highlighted species were intentionally added as mobile predators (see Methodology). Letters represent compact letter display of significant differences between species within each mesocosm (Kruskal-Wallis Rank Sum test): species sharing a letter do not differ significantly after Bonferroni correction.

#### 4.1. Carbon assimilation

Macrofauna colonising OWF turbines is typically rich in filter- and suspension feeders (Degraer et al., 2020), capable of clearing vast amounts of seawater from phytoplankton, zooplankton and/or suspended detritus (Slavik et al., 2019; Mavraki et al., 2020a). Next to the numerically dominant filter- and suspension feeders, these colonising communities include many feeding strategies, which is reflected in a variable food web complexity and trophic redundancy along the vertical depth gradient of the OWF foundations (Mavraki et al., 2020b). This diversity in feeding strategies across the epifaunal community, including different trophic levels and relying directly (direct feeding) or indirectly (feeding on deposits or on phytoplankton grazers) on the uptake of a wide variety of phytoplankton (*in situ*) or the added  $^{13}\text{C}$  labelled *I. galbana* stock (this study), was corroborated here through significant differences between species in their biomass-specific carbon assimilation within mesocosms.

In the CTRL mesocosm, individual carbon assimilation was highest for the common slipper limpet *C. fornicata* and the blue mussel *M. edulis* (as was already observed before by Mavraki et al. (2020a)), and the long-clawed porcelain crab *P. longicornis*. The limpet and mussel both feed directly on the  $^{13}\text{C}$  labelled algae, while *P. longicornis* is known to opportunistically feed on *M. edulis* pseudofaeces (Tenore and González, 1975).

Compared to CTRL, mean carbon assimilation of (added) algal carbon in CC had increased, as more species showed a relatively high carbon assimilation, in excess of 2.00 % of their biomass carbon. Alongside *P. longicornis* and *M. edulis*, the CC mesocosm supported the amphipods *J. herdmani* and *M. acherusicum*, as well as the flatworm *L. tremellaris* as top consumers in terms of carbon assimilation. The amphipods feed directly on suspended organic material (phyto- and zooplankton, as well as detritus; Dixon and Moore, 1997), while *L. tremellaris* preys on those primary consumers (Jennings, 1957). Individual carbon assimilation of *J. herdmani* measured in CC was 100-fold higher compared to that observed before in a similar CTRL environment (Mavraki et al., 2020a), most likely due to an increased feeding rate in a climate change environment (Voet et al., 2021). Such an increased carbon assimilation by suspension feeding phytoplankton consumers could further explain the relatively high carbon assimilation observed in organisms preying on them, such as *L. tremellaris* in the CC mesocosm. Additionally, well-fed *M. edulis* individuals produce (pseudo) faeces containing closely packed undigested algal cells (Riisgård et al., 2011), which could further explain the relatively high carbon assimilation in CC by organisms feeding on those deposits, such as *P. longicornis*, compared to the CTRL environment. Compared to CTRL, the OWF AHS community in this future climate scenario thus maintained a higher mean carbon assimilation and was dominated by species with different feeding strategies.

In the future climate aquaculture scenario (CC + AQ), a similar mix of suspension feeding phytoplankton consumers, deposit feeders and even more predatory species featured among this mesocosm's major consumers. The amphipods *J. herdmani* and *M. acherusicum*, the flatworm *L. tremellaris*, the mussel *M. edulis* and the starfish *A. rubens* were the topmost (added) phytoplankton carbon assimilating species in the CC + AQ treatment. In addition to *L. tremellaris* feeding on i.a. amphipods (Jennings, 1957), *A. rubens* is an active predator with a preference for bivalves (such as *M. edulis*; De Mesel et al., 2013). In the CC + AQ mesocosm, these predators thus had ample food sources available. Overall, however, the mean carbon assimilation was lower in CC + AQ compared to the other mesocosms, most likely caused by an increased competition for a limited food source, both inter- and intraspecific.

*In situ*, the ability of *M. edulis* to filter large volumes of water could potentially lead to a similar food limitation if the system's clearance rate exceeds the food renewal by advection/mixing of the water column and on an ecosystem scale, if influx from outside the system or primary production within the system would be surpassed by the filtration capacity of the *M. edulis* standing stock (Heip et al., 1995). In the BPNS, we hypothesise several feedback loops would prevent the aquaculture biomass within an OWF from reaching such a critical point as to cause a local ecosystem

collapse. Close to the system's carrying capacity, the *M. edulis* individuals would likely no longer continue to grow to a desired commercial size within the usual time frame, indicating the need for downsizing the aquaculture set-up. This was reflected in the CC + AQ mesocosm, where an increased total *M. edulis* biomass generally resulted in a lower overall biomass-specific carbon assimilation.

#### 4.2. Mesocosm carbon budget

Two sampling events took place after addition of  $^{13}\text{C}$  labelled algae to the three mesocosms: one after five days and one after 12 days. By sampling two 'OWF systems' in the first event, carbon assimilated by these systems thus far was partly removed and the abundances and potential competition for resources changed towards the second sampling event. Both datasets, one from each sampling event, were therefore analysed accordingly. At the end of the experiment, an average ( $\pm$ SD) of  $26.8 \pm 2.0$  % of the total added carbon budget was assimilated by the organisms present in the mesocosms. This fraction is relatively high compared to similar studies done on soft sediments, where faunal assimilation typically ranges between 10 % and 25 % (Woulds et al., 2016; Braeckman et al., 2019). Most of the assimilated carbon, across all three mesocosms, was found in *M. edulis*, accounting for  $96.3 \pm 1.1$  % of all assimilated carbon by organisms and  $26.4 \pm 2.2$  % of the total algal carbon added to the mesocosms. This can be explained by the combination of the relatively high carbon assimilation rate of this species (although significantly lower in CC + AQ), the feeding type ('direct' filter feeder) and the high total biomass in all three environmental scenarios. This also reflects the natural *in situ* situation in which *M. edulis* is capable of significantly reducing the primary producer standing stock (Slavik et al., 2019), because of its generally high energy demands (Joschko et al., 2008) and subsequent high clearance rates (Prins et al., 1991; Voet et al., 2021).

The total carbon assimilation by the OWF colonising fauna was slightly higher in the CC environment, likely due to an overall higher mean individual carbon assimilation, compared to CTRL. The highest total carbon assimilation was found in the presence of added *M. edulis* aquaculture biomass (CC + AQ). A stronger increase in CC was likely absent due to a 'distributed success' situation, where some species benefitted from the climate change environment (i.a. *J. herdmani* and *M. senile*) and others did not (i.a. benthic *A. rubens*), balancing each other out. Additionally, it is likely (although not measured here) that mortality of some key colonising species increased due to prolonged exposure to CC conditions (Voet et al., 2021), further weakening the increase of total CC carbon assimilation. Similarly, total carbon assimilation in the CC + AQ environment was presumably balanced out by the overall lower individual carbon assimilation (including that of the abundant *M. edulis*). Moreover, the *M. edulis* standing stock in an OWF could increase substantially by introducing multifunctional co-use of blue mussel aquaculture, meaning the quadrupled *M. edulis* biomass in CC + AQ, compared to CTRL, is on the conservative side (Buck et al., 2010; Voet et al., in prep.).

Across all three mesocosms, the predators/omnivores *L. holsatus*, *A. rubens* and *P. miliaris* were the follow-up species in terms of highest total carbon assimilation of the macrofauna. Noticeably, *M. edulis* has a link with all these species, be it trophic (as prey) and/or non-trophic (as habitat-forming species for potential prey), demonstrating again the ecosystem engineering role of *M. edulis* in a North Sea OWF AHS ecosystem (Krone et al., 2017; Degraer et al., 2020).

Next to the carbon assimilation recovered in the sampled macrofauna, an additional (mean  $\pm$  SD)  $1.4 \pm 1.3$  % and  $4.9 \pm 2.3$  % of the added algal carbon was found in the water and sediment fraction of the mesocosms, respectively. These additional fractions reflect the amount of added algae carbon contained in microbial biomass, leftover microalgae, detrital SPOM (suspended particulate organic matter) and meiofauna. The recovered carbon fraction in CC sediment was roughly double that of what was sampled in CTRL and CC + AQ sediment, likely the result of the increased feeding rates and concurrent flow of organic matter towards the sediment (Lefaille et al., 2018; Slavik et al., 2019; Ivanov et al., 2021).



This was reflected in the observed increase in TOC in CC sediment towards the end of the experiment. While similar sediment enrichment could be expected in the CC + AQ mesocosm because of the considerably higher biomass of suspension feeders, the significantly higher SCOC rates in CC + AQ can explain why this additional sediment carbon fraction was most likely already respired. The estimated total carbon remineralisation by sediment communities was approximately three times higher in CC + AQ compared to CC, suggesting high stimulation of microbial activity following sediment enrichment. Similar high oxygen consumption and mineralisation rates in organic-rich sediments underneath bivalve aquaculture sites were observed before (Christensen et al., 2003; Lunstrum et al., 2018; Ray et al., 2020). Although the fraction of recovered carbon in CC was high, indicating organic sediment enrichment, CC mineralisation rates were low. Previous studies reported a similar decrease in SCOC and (de)nitrification rates in acidified environments, possibly resulting from acidification-induced changes in microbial activity and composition (Braeckman et al., 2014; Wannicke et al., 2018). While our results thus support these observations in the CC mesocosm, the opposite was observed in CC + AQ. As there was no clear difference in sediment macrofauna composition between treatments, the most plausible argument for this discrepancy would be the presence of a large *M. edulis* stock in this treatment. Our results suggest that the stimulating effect of bivalve aquaculture on sediment biogeochemistry counteracts the negative effect of climate change, possibly explaining the absence of sediment enrichment in CC + AQ.

#### 4.3. OWFs and aquaculture in multifunctional co-use

Be it in a current or future climate, as a key species in an OWF AHS community or as a combined multi-use aquaculture target species, the importance of *M. edulis* within this ecosystem is evident. Since over 50 % of annual worldwide mussel aquaculture harvest is produced in Europe and the demand for bivalve consumption products has long exceeded the supply from natural fisheries, aquaculture installations are progressively moving offshore, where space and adequate settlement opportunities are readily available (Smaal, 2002; FAO, 2007; Buck et al., 2010).

As OWFs are proliferating across Europe in aid of its transition towards a fully decarbonised European power system, combining renewable energy structures with nature conservation (Degraer et al., 2020) and aquaculture makes for a sensible argument (IEA, 2019; Steins et al., 2021). The 'multifunctional co-use' of space and infrastructure between OWFs and mussel aquaculture has many advantages: i.a. limiting the total spatial extent of human activities (Michler-Cieluch et al., 2009a; Steins et al., 2021), cutting costs by sharing means and facilities (Michler-Cieluch et al., 2009b; Buck et al., 2010) and minimising the risks associated with high-energy offshore environments through solid attachment possibilities for aquaculture structures (Buck et al., 2006; Buck and Langan, 2017).

Nevertheless, the subsistence of aquaculture in OWFs is highly dependent on biophysical and ecological conditions (i.a. temperature and food availability). Additionally, the presence of an aquaculture set-up substantially increases the filtration capacity towards the top of the water column and the production carrying capacity is only sustainable if organic matter extraction by the mussels is balanced with ecosystem food replenishment. The introduction of bivalve aquaculture will therefore undoubtedly affect, and in turn be affected by, the local ecosystem (Cranford, 2019; Costello et al., 2020). Moreover, such a multifunctional co-use could even alter or exacerbate potential climate change effects on the OWF AHS ecosystem functioning. Indeed, this study identified varied functional (i.e. successful feeding types) and structural (i.e. topmost consumers) changes when exposing the OWF ecosystem to future climate conditions with or without the additional presence of blue mussel aquaculture.

#### 4.4. Methodological constraints

Several measures were taken to create mesocosms that accurately reflect the natural species composition of the OWF ecosystem (De Mesel et al., 2013; Kerckhof et al., 2019; Mavraki et al., 2020a), with little

variation between them. Yet, differences in species composition and abundance between mesocosms at the start of the experiment were observed. These differences resulted from the random distribution of the colonised AHS panels and sediment containers across the environmental treatments. Although logistically not possible within the scope of this study, future experiments would benefit from deploying more AHS panels and/or an *in situ* selection procedure based on the degree of colonisation. Additionally, similar species composition and abundances between mesocosms could have been obtained by collecting single organisms from the AHS panels and sediment communities and adding them to the different mesocosms one by one. By disturbing the organisms in such a way, possible stress reactions could have significantly impacted the feeding behaviour and thus the results of this study. Therefore, collected AHS panels and sediments were left undisturbed and were transferred to the mesocosms as is.

Furthermore, the relative biomass of species in the experimental mesocosms was not necessarily representative of that found in OWF AHS ecosystems. The amphipods *J. herdmanni* and *M. acherusicum* were heavily underrepresented in the mesocosms compared to *in situ* OWF communities in early succession stages (up to five years post-construction; Kerckhof et al., 2019) and even absent in CTRL. Most likely, this was due to a high mortality as seen in relatively long-term experimental conditions (Beermann and Purz, 2013). Additionally, a higher mortality in the climate change environment was expected, as amphipods are sensitive to changes in seawater temperature and/or pH (Poulin and Mouritsen, 2006; Jakob et al., 2016; Voet et al., 2021). Tube-building amphipods are among the most important suspension feeders in the OWF ecosystem and *J. herdmanni* was responsible for the largest share of total carbon assimilation in a similar short-term AHS CTRL experiment (Mavraki, 2020; Mavraki et al., 2020a). Most likely, the contribution of *J. herdmanni* to the total carbon assimilation of AHS colonising fauna would have been equally substantial in this study's CTRL environment, as this species can reach extremely high local densities (Mavraki et al., 2020a). Under climate change conditions, Voet et al. (2021) reported increased clearance rates for *J. herdmanni*, reflected in this study as the mean carbon assimilation of *J. herdmanni* being among the highest of all species present in CC and CC + AQ. However, *in situ*, the high mortality rate of amphipods under climate change (Poulin and Mouritsen, 2006; Jakob et al., 2016; Voet et al., 2021) would likely lessen the relative importance of their functional role within the ecosystem. Likewise, an increased mortality rate most likely further downplayed the relative contribution of an already underrepresented *J. herdmanni* to the total CC and CC + AQ carbon assimilation.

The relative abundance of the plumose anemone *M. senile*, together with that of the common starfish *A. rubens* and the green sea urchin *P. miliaris*, was unintentionally low compared to actual *in situ* AHS ecosystems (De Mesel et al., 2013; De Backer et al., 2020). The first is one of the dominant AHS colonising species in the North Sea (Degraer et al., 2020; De Backer et al., 2020) and the latter are both among the most conspicuous mobile predators found on the OWF foundations. An underestimation of predator abundances in the experiments could be the result of a random *in situ* distribution during sampling by the diving team and/or increased mortality due to climate change stressors. This underestimation probably affected the predation pressure in the mesocosms, as well as the competition between and within predatory species, compared to *in situ* conditions. The low anemone and urchin abundances were most likely a combined result of low numbers on the *in situ* sampled AHS plates and a sensitivity of these species to (prolonged) climate change conditions (Suckling et al., 2020; Voet et al. 2021). The starfish *A. rubens* is less susceptible to acidification (McCarthy et al., 2020), so low experimental numbers were most likely a result of random distribution while sampling.

Similar to what was observed in the CC + AQ mesocosm, home to most *M. senile*, *A. rubens* and *P. miliaris* individuals, predatory species would have most likely played a more prominent role in total assimilation budgets of all mesocosms.

Finally, the added value of a fully crossed experimental set-up between climate change and aquaculture scenarios in unravelling and uncoupling the effects of both stressors on the OWF AHS colonising community is

evident. However, even though logistic limitations within this project prevented the execution of such a set-up, this study was still able to distil valuable insights into the structure and functioning of an OWF ecosystem in different climate and multi-use scenarios. The obtained carbon assimilation rates also offer possibilities for informative extrapolation exercises (see below). Furthermore, the experimental work performed in this study was innovative in its use of pulse-chase techniques on an ecosystem-wide scale in current and future climate settings. The use of large, environmentally manipulated mesocosms allowed us to incorporate many species interactions (e.g. predation and competition) and capture direct and indirect effects (e.g. on filter- and detritus feeders, respectively), therefore proving to be highly relevant on an ecological scale. Additionally, this approach acknowledged the benthic-pelagic coupling and permitted it to be studied in different climate and aquaculture scenarios.

#### 4.5. From mesocosm to monopile: extrapolating ecological effects

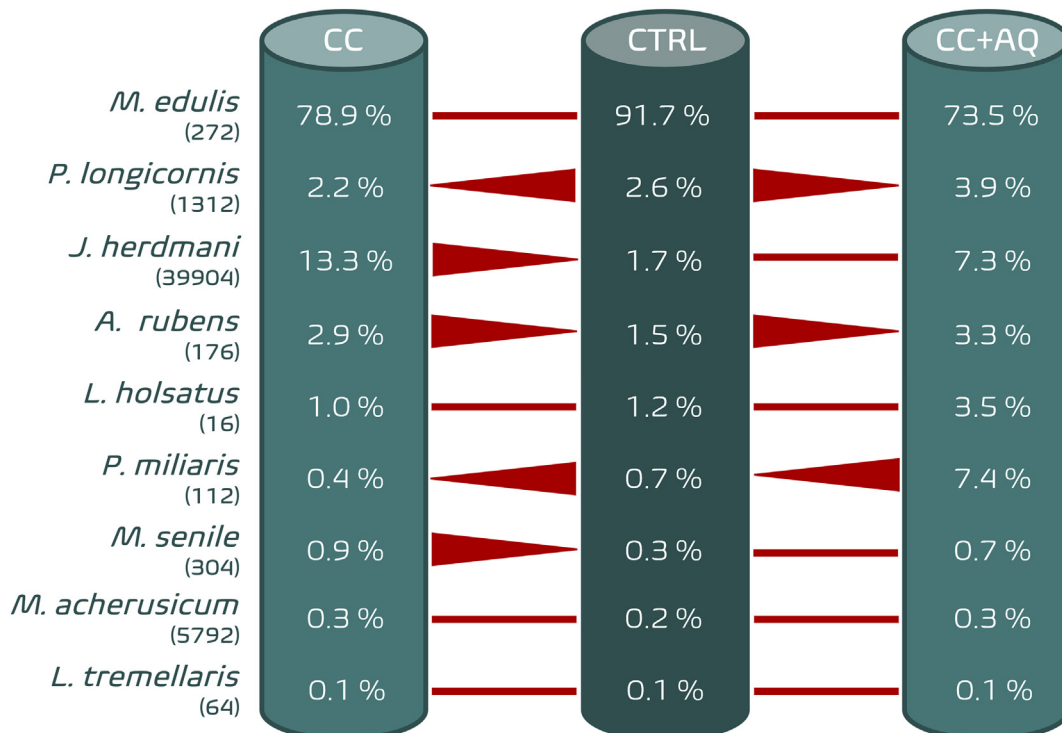
We present here a first and approximative extrapolation exercise describing the effects of climate change and aquaculture on a natural OWF turbine foundation community. The obtained carbon assimilation rates for the different OWF colonising species were combined with *in situ* abundance data of monopile foundations in a Belgian OWF, collected between 2009 and 2019 (Zupan M., pers. comm.). Abundance data was available for nine of the mesocosm species and was used to populate a hypothetical OWF AHS community, identical for each of the three environmental scenarios (CTRL, CC and CC + AQ). Using this study's results and the aforementioned *in situ* abundances, the total carbon assimilation [C] of the OWF AHS community and the relative contribution and importance (rank) of each species were calculated in each climate scenario (Fig. 5). Because unavailable in this study, carbon assimilation of amphipods in CTRL was based on Mavraki et al. (2020a). To simplify this extrapolation

exercise, mortality due to the different environmental conditions and vertical zonation of species were not taken into account.

Even though its relative contribution decreased in both climate change scenarios (CC and CC + AQ), *M. edulis* remained the number one species in terms of carbon assimilation in all three environments (indicated by straight lines in Fig. 5). Climate change has a stimulatory effect on carbon assimilation, as the relative contribution of species (other than mussels) to the extrapolated total carbon assimilation generally increased in CC and CC + AQ. More 'winners' (increase in rank, indicated by outward wedges in Fig. 5) were to be found in CC compared to CC + AQ, demonstrating again the increased competition between species in an aquaculture environment. Whereas simplifications such as the lack of discrimination between mortality rates abate the level of detail in this extrapolation, potential sampling bias was eliminated by using an identical turbine foundation community in each of the three environmental scenarios. A rudimentary exercise such as this one clearly shows the potential of experimental datasets like the one presented in this study to provide an insight into the structure and functioning of an OWF ecosystem in different parallel climate and aquaculture scenarios. This is sorely needed to anticipate the critical juncture where technical and legislative complexities of implementing aquaculture in multifunctional co-use with offshore renewable energy might be overshadowed by the global and economic impact of climate change.

## 5. Conclusion

This study identified the blue mussel *M. edulis* as the most impactful OWF AHS species in terms of (total) carbon assimilation. Climate change significantly affected the carbon flow through the OWF food web: carbon assimilation by macrofauna species and the resulting 'top consumers' differed significantly between the climate scenarios, likely as a result of dynamic trophic and non-trophic links between *M. edulis* and other consumers. This impact was echoed in the enriched sediments present in



**Fig. 5.** Relative contribution of nine macrofauna species to the extrapolated total carbon assimilation of an identical hypothetical OWF AHS community in three environmental scenarios (CTRL: control; CC: climate change; CC + AQ: climate change with aquaculture). Mean macrofauna densities [ind  $m^{-2}$ ] are indicated between brackets and are based on *in situ* survey data (2009–2019; Zupan M., pers. comm.). Connections between monopile foundations represent relative importance of species in the respective scenarios, where straight lines indicate equal rank order in terms of relative contribution and wedges indicate an increase or decrease in rank order compared to that in CTRL.

the climate change scenario, illustrating the ecosystem-wide reach of these effects. Additionally, the presence of blue mussel aquaculture induced a higher level of inter- and intraspecific competition, further demonstrating that the filtration capacity of the *M. edulis* aquaculture standing stock can influence the nearby OWF AHS ecosystem. Finally, whereas the concept of OWFs and aquaculture in multifunctional co-use should be endorsed on the marine spatial planning agenda, it should be done alongside studies towards its ecosystem impact in current and future climate scenarios.

### CRedit authorship contribution statement

**Hee Voet:** Conceptualization, Methodology, Validation, Formal analysis, Investigation, Resources, Data curation, Writing – original draft, Writing – review & editing, Visualization. **E. Vlamincx:** Conceptualization, Methodology, Validation, Formal analysis, Investigation, Resources, Data curation, Writing – original draft, Writing – review & editing. **C. Van Colen:** Conceptualization, Methodology, Validation, Resources, Writing – review & editing, Supervision, Funding acquisition. **S. Bodé:** Methodology, Formal analysis, Writing – review & editing. **P. Boeckx:** Funding acquisition, Resources, Writing – review & editing. **S. Degraer:** Funding acquisition, Resources, Writing – review & editing. **T. Moens:** Methodology, Validation, Resources, Writing – review & editing, Supervision, Project administration. **J. Vanaverbeke:** Conceptualization, Methodology, Validation, Resources, Writing – review & editing, Supervision, Project administration, Funding acquisition. **U. Braeckman:** Conceptualization, Methodology, Validation, Resources, Writing – review & editing, Supervision.

### Data availability

Data will be made available on request.

### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

### Acknowledgements

The research leading to results presented in this publication was funded through BELSPO BRAIN-be project BR/175/A1/PERSUADE, additional funding obtained from Ghent University's Special Research Fund (BOF) through GOA project 01G02617 and carried out with infrastructure funded by EMBRC Belgium FWO project GOH3817N. This work was further supported by data and infrastructure provided by VLIZ as part of the Flemish contribution to LifeWatch and by logistic support from the Research Vessel Simon Stevin and the scientific diving teams of VLIZ and RBINS. Practical and analytical support by the MarBioL Research Group (UGent) and the Isotope Bioscience Laboratory (ISOFYS; UGent) was indispensable in the realisation of this study.

### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2022.159285>.

### References

Banas, N.S., Hickey, B.M., Newton, J.A., Ruesink, J.L., 2007. Tidal exchange, bivalve grazing, and patterns of primary production in Willapa Bay, Washington, USA. *Mar. Ecol. Prog. Ser.* 341, 123–139.

Baretta-Bekker, J.G., Baretta, J.W., Latuhihin, M.J., Desmit, X., Prins, T.C., 2009. Description of the long-term (1991–2005) temporal and spatial distribution of phytoplankton carbon biomass in the dutch North Sea. *J. Sea Res.* 61, 50–59. <https://doi.org/10.1016/j.seares.2008.10.007>.

Beermann, J., Purz, A.K., 2013. Comparison of life history parameters in coexisting species of the genus *Jassa* (Amphipoda, Ischyroceridae). *J. Crustac. Biol.* 33 (6), 784–792.

Bereiter, B., Eggleston, S., Schmitt, J., Nehrbass-Ahles, C., Stocker, T.F., Fischer, H., Kipfstuhl, S., Chappellaz, J., 2015. Revision of the EPICA dome C CO<sub>2</sub> record from 800 to 600-kyr before present. *Geophys. Res. Lett.* 42 (2), 542–549.

Bindoff, N.L., WWL, Cheung, Kairo, J.G., Aristegui, J., Guinder, V.A., Hallberg, R., Hilmi, N., Jiao, N., Karim, M.S., Levin, L., O'Donoghue, S., Purca Cuicapusa, S.R., Rinkevich, B., Suga, T., Tagliabue, A., Williamson, P., 2019. Changing ocean, marine ecosystems, and dependent communities. In: Pörtner, H.O., Roberts, D.C., Masson-Delmotte, V., Zhai, P., Tignor, M., Poloczanska, E., Mintenbeck, K., Alegría, A., Nicolai, M., Okem, A., Petzold, J., Rama, B., Weyer, N.M. (Eds.), IPCC Special Report on the Ocean and Cryosphere in a Changing Climate.

Braeckman, U., Van Colen, C., Guilini, K., Van Gansbeke, D., Soetaert, K., Vincx, M., Vanaverbeke, J., 2014. Empirical evidence reveals seasonally dependent reduction in nitrification in coastal sediments subjected to near future ocean acidification. *PLoS One* 9 (10), e108153. <https://doi.org/10.1371/journal.pone.0108153>.

Braeckman, U., Pasotti, F., Vázquez, S., Zacher, K., Hoffmann, R., Elvert, M., Marchant, H., Buckner, C., Quartino, M.L., Cormack, W.M., Soetaert, K., Wenzhöfer, F., Vanreusel, A., 2019. Degradation of macroalgal detritus in shallow coastal Antarctic sediments. *Limnol. Oceanogr.* 64, 1423–1441.

Braeckman, U., Lefaible, N., Bruns, E., Moens, T., 2020. Turbine-related impacts on macrobenthic communities: an analysis of spatial and temporal variability. In: Environmental Impacts of Offshore Wind Farms in the Belgian Part of the North Sea: Empirical Evidence Inspiring Priority Monitoring, Research and Management. Series 'Memoirs on the Marine Environment'. Royal Belgian Institute of Natural Sciences, OD Natural Environment, Marine Ecology and Management, Brussels, pp. 61–78 131 pp.

Breine, N.T., De Backer, A., Van Colen, C., Moens, T., Hostens, K., Van Hoey, G., 2018. Structural and functional diversity of soft-bottom macrobenthic communities in the southern North Sea. *Estuar. Coast. Shelf Sci.* 214, 173–184.

Breteler, W.C.M., Grice, K., Schouten, S., Kloosterhuis, H.T., Damsté, J.S.S., 2002. Stable carbon isotope fractionation in the marine copepod *Temora longicornis*: unexpectedly low  $\delta^{13}C$  value of faecal pellets. *Mar. Ecol. Prog. Ser.* 240, 195–204.

Buck, B.H., Langan, R., 2017. Chapter 14: epilogue—pathways towards sustainable ocean food production. In: Buck, B.H., Langan, R. (Eds.), *Aquaculture Perspective of Multi-Use Sites in the Open Ocean*, pp. 395–404 413 pp.

Buck, B.H., Berg-Pollack, A., Assheuer, J., Zielinski, O., Kassen, D., 2006. Technical realization of extensive aquaculture constructions in offshore wind farms: consideration of the mechanical loads. Proceedings of the 25th International Conference on Offshore Mechanics and Arctic Engineering (OMAE 2006). American Society of Mechanical Engineers, pp. 1–7.

Buck, B.H., Ebeling, M.W., Michler-Cieluch, T., 2010. Mussel cultivation as a co-use in offshore wind farms: potential and economic feasibility. *Aquac. Econ. Manag.* 14 (4), 255–281.

Cabre, L.M., Hosegood, P., Attrill, M.J., Bridger, D., Sheehan, E.V., 2021. Offshore longline mussel farms: a review of oceanographic and ecological interactions to inform future research needs, policy and management. *Rev. Aquac.* 1–24.

Christensen, P.B., Glud, R.N., Dalsgaard, T., Gillespie, P., 2003. Impacts of longline mussel farming on oxygen and nitrogen dynamics and biological communities of coastal sediments. *Aquaculture* 218 (1), 567–588. [https://doi.org/10.1016/S0044-8486\(02\)00587-2](https://doi.org/10.1016/S0044-8486(02)00587-2).

Coates, D.A., Deschutter, Y., Vincx, M., Vanaverbeke, J., 2014. Enrichment and shifts in macrobenthic assemblages in an offshore wind farm area in the Belgian part of the North Sea. *Mar. Environ. Res.* 95, 1–12.

Costello, C., Cao, L., Gelcich, S., Cisneros-Mata, M.A., Free, C.M., Froehlich, H.E., Golden, C.D., Ishimure, G., Maier, J., Macadam-Somer, I., Mangin, T., Melnychuk, M.C., Miyahara, M., de Moor, C.L., Naylor, R., Nøstbakken, L., Ojeda, E., O'Reilly, E., Parma, A.M., Plantinga, A.J., Thilsted, S.H., Lubchenko, J., 2020. The future of food from the sea. *Nature* 588, 95–100.

Cranford, P.J., 2019. Chapter 8: Magnitude and Extent of Water Clarification Services Provided by Bivalve Suspension Feeding. In: Smaal, A.C., Ferreira, J.G., Grant, J., Petersen, J.K., Strand, Ø. (Eds.), *Goods and Services of Marine Bivalves*, pp. 119–141 598 pp.

De Backer, A., Buyse, J., Hostens, K., 2020. A decade of soft sediment epibenthos and fish monitoring at the Belgian offshore wind farm area. In: Degraer, S., Brabant, R., Rumes, B., Vigin, L. (Eds.), *Environmental Impacts of Offshore Wind Farms in the Belgian Part of the North Sea: Empirical Evidence Inspiring Priority Monitoring, Research and Management*. Royal Belgian Institute of Natural Sciences, OD Natural Environment, Marine Ecology and Management, pp. 79–113 133 pp.

De Borger, E., Ivanov, E., Capet, A., Braeckman, U., Vanaverbeke, J., Grégoire, M., Soetaert, K., 2021. Offshore windfarm footprint of sediment organic matter mineralization processes. *Front. Mar. Sci.* 8, 632243. <https://doi.org/10.3389/fmars.2021.632243>.

De Mesel, I., Kerckhof, F., Rumer, B., Norro, A., Houziaux, J.-S., Degraer, S., 2013. Fouling community on the foundations of wind turbines and the surrounding scour protection. In: Degraer, S., Brabant, R., Rumes, B. (Eds.), *Environmental Impacts of Offshore Wind Farms in the Belgian Part of the North Sea: Learning from the Past to Optimise Future Monitoring Programmes*. Royal Belgian Institute of Natural Sciences, Operational Directorate Natural Environment, Marine Ecology and Management, Brussels, pp. 122–137 239 pp.

Degraer, S., Carey, D.A., JWP, Coolen, Hutchison, Z.L., Kerckhof, F., Rumes, B., Vanaverbeke, J., 2020. Offshore wind farm artificial reefs affect ecosystem structure and functioning: A synthesis. In: Special issue on understanding the effects of offshore wind energy development on fisheries. *Oceanography* 33 (4), 48–57.

Environmental impacts of offshore wind farms in the Belgian part of the north sea: attraction, avoidance and habitat use at various spatial scales. In: Degraer, S., Brabant, R., Rumes, B., Vigin, L. (Eds.), *Memoirs on the Marine Environment*. Royal Belgian Institute of Natural Sciences, OD Natural Environment, Marine Ecology and Management, Brussels 104 pp.

Dixon, I.M.T., Moore, P.G., 1997. A comparative study on the tubes and feeding behaviour of eight species of corophioid amphipoda and their bearing on phylogenetic relationships within the corophioidea. *Philos. Trans. R. Soc., B* 352, 93–112.

Dumbauld, B.R., Ruesink, J.L., Rumrill, S.S., 2009. The ecological role of bivalve shellfish aquaculture in the estuarine environment: a review with application to oyster and clam culture in west coast (USA) estuaries. *Aquaculture* 290 (3–4), 196–223.



- Dupont, S., Pörtner, H., 2013. Marine science: get ready for ocean acidification. *Nature* 498 (7455), 429.
- Fabry, V.J., Seibel, B.A., Feely, R.A., Orr, J.C., 2008. Impacts of ocean acidification on marine fauna and ecosystem processes. *ICES J. Mar. Sci.* 65 (3), 414–432.
- FAO, 2007. Aquaculture production: values 1984–2005. FISHSTAT Plus - Universal software for fishery statistical time series. Fishery Information, Data and Statistics Unit. Food and Agriculture Organization of the United Nations, Rome, Italy.
- Faulkner, H., 2013. Influence of Aquaculture on Winter Sea Duck Distribution and Abundance in South Puget Sound. The Evergreen State College, Washington MSc thesis.
- Gallardi, D., 2014. Effects of bivalve aquaculture on the environment and their possible mitigation: a review. *Fish. Aquac.* 5 (3), 9.
- GWEC (Global Wind Energy Council), 2021. In: Lee, J., Zhao, F., Dutton, A., Backwell, B., Fiestas, R., Qiao, L., Balachandran, N., Lim, S., Liang, W., Clarke, E., Lathigara, A., Younger, D.R. (Eds.), *Global Wind Report 2021* 80pp.
- Harris, D., Horwath, W., van Kessel, C., 2001. Acid fumigation of soils to remove carbonates prior to total organic carbon or carbon-13 isotopic analysis. *Soil Sci. Soc. Am. J.* 65. <https://doi.org/10.2136/sssaj2001.1853>.
- Heip, C.H.R., Goosen, N.K., Herman, P.M.J., Kromkamp, J., Middelburg, J., Soetaert, K., 1995. Production and consumption of biological particles in temperate tidal estuaries. *Oceanogr. Mar. Biol. Annu. Rev.* 33, 1–149.
- IEA (International Energy Agency), 2019. “Offshore wind outlook”, by Dr. Fatih Birol (Ex. Dir. IEA) on 25 October 2019, Copenhagen, Denmark.
- IPCC, 2021. Summary for policymakers. In: Masson-Delmotte, V., Zhai, P., Pirani, A., Connors, S.L., Péan, C., Berger, S., Caud, N., Chen, Y., Goldfarb, L., Gomis, M.L., Huang, M., Leitzell, K., Lonnoy, E., JBR, Matthews, Maycock, T.K., Waterfield, T., Yelekçi, O., Yu, R., Zhou, B. (Eds.), *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press In Press.
- Ivanov, E., Capet, A., De Borger, E., Degraer, S., Delhez, E.J.M., Soetaert, K., Vanaverbeke, J., Grégoire, M., 2021. Offshore wind farm footprint on organic and mineral particle flux to the bottom. *Front. Mar. Sci.* 8, 631799.
- Jakob, L., Axenov-Gribanov, D.V., Gurkov, A.N., Ginzburg, M., Bedulina, D.S., Timofeyev, M.A., Luckenbach, T., Lucassen, M., Sartoris, F.J., Pörtner, H.-O., 2016. Lake baikal amphipods under climate change: thermal constraints and ecological consequences. *Ecosphere* 7 (3), e01308.
- Jennings, J.B., 1957. Studies on feeding, digestion, and food storage in free-living flatworms (Platyhelminthes: Turbellaria). *Biol. Bull.* 112 (1), 63–80.
- Joschko, T.J., Buck, B.H., Gutow, L., Schröder, A., 2008. Colonization of an artificial hard substrate by *Mytilus edulis* in the german bight. *Mar. Biol.* 152, 350–360.
- Kerckhof, F., Rumes, B., Degraer, S., 2019. About “mytilisation” and “slimeification”: A decade of succession of the fouling assemblages on wind turbines off the Belgian coast. In: Degraer, S., Brabant, R., Rumes, B., Vigin, L. (Eds.), *Environmental Impacts of Offshore Wind Farms in the Belgian Part of the North Sea: Marking a Decade of Monitoring, Research and Innovation*. Royal Belgian Institute of Natural Sciences, OD Natural Environment, Marine Ecology and Management, pp. 73–84.
- Krone, R., Dederer, G., Kanstinger, R., Krämer, P., Schneider, C., 2017. Mobile demersal mega-fauna at common offshore wind turbine foundations in the german bight (North Sea) two years after deployment – increased production rate of cancer pagurus. *Mar. Environ. Res.* 123, 53–61.
- Lefaille, N., Braeckman, U., Moens, T., 2018. Effects of wind turbine foundations on surrounding macrobenthic communities. In: Degraer, S., Brabant, R., Rumes, B., Vigin, L. (Eds.), *Environmental Impacts of Offshore Wind Farms in the Belgian Part of the North Sea: Assessing and Managing Effect Spheres of Influence*. Royal Belgian Institute of Natural Sciences, OD Natural Environment, Marine Ecology and Management, pp. 57–77 136 pp.
- LifeWatch Belgium, 2015. Thornton Measuring Buoy (C-Power). Flanders Marine Institute. <https://rshiny.lifewatch.be/buoy-data/>. (Accessed 9 January 2018).
- Lunstrum, A., McGlathery, K., Smyth, A., 2018. Oyster (*Crassostrea virginica*) aquaculture shifts sediment nitrogen processes toward mineralization over denitrification. *Estuar. Coasts* 41 (4), 1130–1146. <https://doi.org/10.1007/s12237-017-0327-x>.
- Lüthi, D., Le Floch, M., Bereiter, B., Blunier, T., Barnola, J.-M., Siegenthaler, U., Raynaud, D., Jouzel, J., Fischer, H., Kawamura, K., Stocker, T.F., 2008. High-resolution carbon dioxide concentration record 650,000–800,000 years before present. *Nature* 453 (7193), 379–382.
- Maar, M., Nielsen, T.G., Bolding, K., Burchard, H., Visser, A.W., 2007. Grazing effects of blue mussel *Mytilus edulis* on the pelagic food web under different turbulence conditions. *Mar. Ecol. Prog. Ser.* 339, 199–213.
- Maar, M., Bolding, K., Petersen, J.K., Hansen, J.L.S., Timmermann, K., 2009. Local effects of blue mussels around turbine foundations in an ecosystem model of nysted offshore wind farmDenmark. *Journal of Sea Research* 62 (2–3), 159–174.
- Mavraki, N., 2020. On the Food-web Ecology of Offshore Wind Farms, the Kingdom of Suspension Feeders. Ghent University 276 pp.
- Mavraki, N., Degraer, S., Moens, T., Vanaverbeke, J., 2020b. Functional differences in trophic structure of offshore wind farm communities: a stable isotope study. *Mar. Environ. Res.* 157, 13 pp.
- Mavraki, N., Degraer, S., Vanaverbeke, J., Braeckman, U., 2020a. Organic matter assimilation by hard substrate fauna in an offshore wind farm area: a pulse-chase study. *ICES J. Mar. Sci.* <https://doi.org/10.1093/icesjms/fsaa133>.
- Mavraki, N., Degraer, S., Vanaverbeke, J., 2021. Offshore wind farms and the attraction-production hypothesis: insights from a combination of stomach content and stable isotope analyses. *Hydrobiologia* 848 (7), 1639–1657.
- McCarthy, I.D., Whiteley, N.M., Fernandez, W.S., Ragagnin, M.N., Cornwell, T.O., Suckling, C.C., Turra, A., 2020. Elevated pCO<sub>2</sub> does not impair performance in autotomised individuals of the intertidal predatory starfish *Asterias rubens* (Linnaeus, 1758). *Mar. Environ. Res.* 153, 104841. <https://doi.org/10.1016/j.marenvres.2019.104841>.
- Mehrbach, C., Culbertson, C.H., Hawley, J.E., Pytkowicz, R.M., 1973. Measurement of the apparent dissociation constants of carbonic acid in seawater at atmospheric pressure. *Limnol. Ocean.* 18, 897–907.
- Michler-Cieluch, T., Krause, G., Buck, B.H., 2009a. Marine aquaculture within offshore wind farms: social aspects of multiple use planning. *GAIA* 18 (2), 158–162.
- Michler-Cieluch, T., Krause, G., Buck, B.H., 2009b. Reflections on integrating operation and maintenance activities of offshore wind farms and mariculture. *Ocean Coast. Manag.* 52 (1), 57–68.
- MSP – Marine Spatial Plan 2020-2026, 2020. Food Chain Safety and Environment. Marine Environment Service, Federal Public Service – Health. <https://www.health.belgium.be/en/environment/seas-oceans-and-antarctica/north-sea-and-oceans/marine-spatial-plan>. (Accessed 6 January 2021).
- Nagelkerken, I., Munday, P.L., 2016. Animal behaviour shapes the ecological effects of ocean acidification and warming: moving from individual to community-level responses. *Glob. Chang. Biol.* 22 (3), 974–989.
- Ong, E.Z., Briffa, M., Moens, T., Van Colen, C., 2017. Physiological responses to ocean acidification and warming synergistically reduce condition of the common cockle *Cerastoderma edule*. *Mar. Environ. Res.* 130, 38–47.
- Pierrot, D., Lewis, E., DWR, Wallace, 2006. MS excel program developed for CO<sub>2</sub>System calculations. ORNL/CDIAC-105a. Carbon Dioxide Inf. Anal. Center, Oak Ridge Natl. Lab. US Dep. Energy, Oak Ridge, Tennessee 413 pp.
- Pörtner, H.O., Langenbuch, M., Reipschläger, A., 2004. Biological impact of elevated ocean CO<sub>2</sub> concentrations: lessons from animal physiology and earth history. *J. Oceanogr.* 60 (4), 705–718.
- Poulin, R., Mouritsen, K.N., 2006. Climate change, parasitism and the structure of intertidal ecosystems. *J. Helminthol.* 80 (2), 183–191.
- Prins, T.C., Smaal, A.C., Pouwer, A.J., 1991. Selective ingestion of phytoplankton by the bivalves *Mytilus edulis* and *Cerastoderma edule*. *Hydrobiol. Bull.* 25, 93–100.
- Provoost, P., van Heuven, S., Soetaert, K., Laane, R.W.P.M., Middelburg, J.J., 2010. Seasonal and long-term changes in pH in the dutch coastal zone. *Biogeosciences* 7, 3869–3878.
- Ray, N.E., Al-Haj, A., Fulweiler, R.W., 2020. Sediment biogeochemistry along an oyster aquaculture chronosequence. *Mar. Ecol. Prog. Ser.* 646, 13–27. <https://doi.org/10.3354/meps13377>.
- Reubens, J.T., Braeckman, U., Vanaverbeke, J., Van Colen, C., Degraer, S., Vincx, M., 2013. Aggregation at windmill artificial reefs: CPUE of Atlantic cod (*Gadus morhua*) and pouting (*Trisopterus luscus*) at different habitats in the Belgian part of the North Sea. *Fish. Res.* 139, 28–34.
- Riisgård, H.U., Egede, P.P., Saavedra, I.B., 2011. Feeding behaviour of the mussel, *Mytilus edulis*: new observations, with a mini-review of current knowledge. *Journal of Marine Biology* 3, 1–13.
- Rosenblatt, A.E., Schmitz, O.J., 2016. Climate change, nutrition, and bottom-up and top-down food web processes. *Trends Ecol. Evol.* 31 (12), 965–975.
- RStudio Team, 2016. RStudio: Integrated Development for R. RStudio Inc, Boston, MA.
- Schupp, M.F., Bocci, M., Depellegrin, D., Kafas, A., Kyriazi, Z., Lukic, I., Schultz-Zehden, A., Krause, G., Onyango, V., Buck, B.H., 2019. Towards a common understanding of ocean multi-use. *Front. Mar. Sci.* 6, 165.
- Slavik, K., Lemmen, C., Zhang, W., Kerimoglu, O., Klingbeil, K., Wirtz, K.W., 2019. The large-scale impact of offshore wind farm structures on pelagic primary productivity in the southern North Sea. *Hydrobiologia* 845, 35–53.
- Smaal, A.C., 2002. European mussel cultivation along the Atlantic coast: production status, problems and perspectives. *Hydrobiologia* 484, 89–98.
- Sokolova, I.M., Frederich, M., Bagwe, R., Lannig, G., Sukhotin, A.A., 2012. Energy homeostasis as an integrative tool for assessing limits of environmental stress tolerance in aquatic invertebrates. *Mar. Environ. Res.* 79, 1–15.
- Steins, N.A., Veraart, J.A., Klostermann, J.E.M., Poelman, M., 2021. Combining offshore wind farms, nature conservation and seafood: lessons from a dutch community of practice. *Mar. Policy* 126, 104371.
- Strong, A.I., Kroeker, K.J., Teneva, L.T., Mease, L.A., Kelly, R.P., 2014. Ocean acidification 2.0: managing our changing coastal ocean chemistry. *Bioscience* 64 (7), 581–592. <https://doi.org/10.1093/biosci/biu072>.
- Suckling, C.C., Kelly, M.S., Hughes, A.D., Cottier-Cook, E.J., 2020. Chapter 27 – Psammecinus miliaris. In: Lawrence, J.M. (Ed.), *Developments in Aquaculture and Fisheries Science*. 43. Elsevier, pp. 487–496. <https://doi.org/10.1016/B978-0-12-819570-3.00027-5>.
- Tenore, K.R., González, N., 1975. Food chain patterns in the Ría de Arosa, Spain: an area of intense mussel aquaculture. In: Persoone, G., et al. (Eds.), *Proceedings of the 10th European Symposium on Marine Biology, Ostend, Belgium, Sept. 17-23 (1975): Population Dynamics of Marine Organisms in Relation With Nutrient Cycling in Shallow Waters*, pp. 601–619.
- Thomsen, J., Haynert, K., Wegner, K.M., Melzner, F., 2015. Impact of seawater carbonate chemistry on the calcification of marine bivalves. *Biogeosciences* 12 (14), 4209–4220.
- Voet, H.E.E., Van Colen, C., Vanaverbeke, J., 2021. Climate change effects on the ecophysiology and ecological functioning of an offshore wind farm artificial hard substrate community. *Sci. Total Environ.* 810, 152194. <https://doi.org/10.1016/j.scitotenv.2021.152194>.
- Voet et al., in prep., Voet HEE, Vanaverbeke J and Soetaert K (in prep.). Modelling the combined effects of climate change on an offshore wind farm artificial hard substrate community and blue mussel (*Mytilus edulis*) aquaculture in multifunctional co-use. Manuscript in preparation.
- Wannicke, N., Frey, C., Law, C.S., Voss, M., 2018. The response of the marine nitrogen cycle to ocean acidification. *Glob. Change Biol.* 24, 5031–5043. <https://doi.org/10.1111/gcb.14424>.
- WindEurope, 2021. Wind Energy – Powering the European Green Deal. <https://windeurope.org/about-wind/campaigns/european-green-deal/>. (Accessed 16 June 2021).
- Woulds, C., Bouillon, S., Cowie, G.L., Drake, E., Middelburg, J.J., Witte, U., 2016. Patterns of carbon processing at the seafloor: the role of faunal and microbial communities in moderating carbon flows. *Biogeosciences* 13, 4343–4357.
- Žydelis, R., Esler, D., Kirk, M., Boyd, W.S., 2009. Effects of off-bottom shellfish aquaculture on winter habitat use by molluscivorous sea ducks. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 19 (1), 34–42.