



Climate change effects on the ecophysiology and ecological functioning of an offshore wind farm artificial hard substrate community



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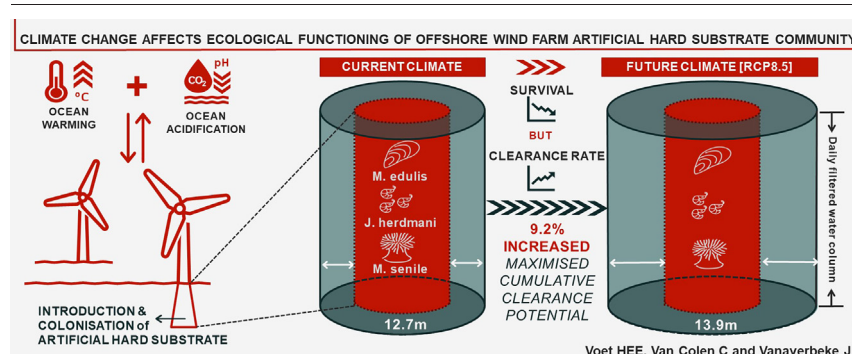
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HIGHLIGHTS

- Local effects of offshore wind farms add to and interact with global climate change.
- Species-specific effects on artificial hard substrate colonising community
- Mortality, feeding and metabolism generally increased with temperature and lower pH
- Temperature and pH had antagonistic effect on growth.
- Maximised cumulative clearance potential significantly increased by climate change

GRAPHICAL ABSTRACT



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ABSTRACT

In the effort towards a decarbonised future, the local effects of a proliferating offshore wind farm (OWF) industry add to and interact with the global effects of marine climate change. This study aimed to quantify potential ecophysiological effects of ocean warming and acidification and to estimate and compare the cumulative clearance potential of suspended food items by OWF epifauna under current and future climate conditions. To this end, this study combined ecophysiological responses to ocean warming and acidification of three dominant colonising species on OWF artificial hard substrates (the blue mussel *Mytilus edulis*, the tube-building amphipod *Jassa herdmanni* and the plumose anemone *Metridium senile*). In general, mortality, respiration rate and clearance rate increased during 3- to 6-week experimental exposures across all three species, except for *M. senile*, who exhibited a lower clearance rate in the warmed treatments (+3 °C) and an insensitivity to lowered pH (-0.3 pH units) in terms of survival and respiration rate. Ocean warming and acidification affected growth antagonistically, with elevated temperature being beneficial for *M. edulis* and lowered pH being beneficial for *M. senile*. The seawater volume potentially cleared from suspended food particles by this AHS colonising community increased significantly, extending the affected distance around an OWF foundation by 9.2% in a future climate scenario. By using an experimental multi-stressor approach, this study thus demonstrates how ecophysiology underpins functional responses to climate change in these environments, highlighting for the first time the integrated, cascading potential effects of OWFs and climate change on the marine ecosystem.

Abbreviations: OWF, offshore wind farm; AHS, artificial hard substrate; GHG, greenhouse gas.

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1. Introduction

The accelerating anthropogenic emission of greenhouse gasses (GHGs) into the atmosphere has global-scale consequences, ocean warming and acidification being among the most pressing for the marine ecosystem (Hoegh-Guldberg et al., 2014; Bindoff et al., 2019). Global average sea surface temperatures (SST) have increased since the 1950s, with the highest average increase in the Atlantic Ocean (0.3 °C per decade since the 1970s) and the fastest warming rates over the European continental shelf areas (including the southern North Sea) (Hoegh-Guldberg et al., 2014). Additionally, oceanic uptake of CO₂ since the 18th century has resulted in a significant acidification of the ocean, with a pH decrease of 0.1 in ocean surface waters over the last 100 years (26% increase in acidity; Hoegh-Guldberg et al., 2014). The International Panel on Climate Change (IPCC) RCP8.5 'business-as-usual'-scenario (Representative Concentration Pathway) predicts an average SST rise of ± 3 °C towards the end of this century and a decrease in surface ocean pH of ± 0.3 , corresponding to a 100% increase in acidity. Furthermore, shallow coastal environments are predicted to be among the most impacted marine habitats, as most of the warming is happening near the surface and as acidification rates up to an order of magnitude higher compared to those for open ocean ecosystems have been observed (Provoost et al., 2010; Strong et al., 2014; Bindoff et al., 2019).

With the awareness of climate change and its pressures on the global economy growing, the incentives for moving towards a more sustainable energy production have pushed an expansion of the offshore wind industry across the planet. The global cumulative offshore wind power capacity is currently up to 35 GW (with another 70 GW expected to be added by 2025), of which $\pm 92\%$ is operated by the current global market leaders Europe and China (± 23 GW and ± 10 GW, respectively; GWEC, 2021). With the European Green Deal, the European Union (EU) has committed to become climate neutral by 2050 and cut GHG emissions by at least 40% below 1990 levels by 2030 (EC, 2018; WindEurope, 2021). As the International Energy Agency aims to have wind as the number one source of power generation in Europe by 2040, offshore wind farms (OWFs) are proliferating across the continent and mainly in the North Sea (IEA, 2019; Degraer et al., 2020). Nonetheless, in this effort to mitigate global climate change, the installation of OWFs introduces large quantities of artificial hard substrate (AHS), fundamentally changing the local (usually soft sediment) marine habitat (Gill et al., 2018; Michaelis et al., 2019). Subsequently, these newly established OWF AHS habitats affect the local ecosystem structure and functioning. Structurally, the submerged OWF foundations are rapidly colonised by habitat-forming epibenthic communities (Krone et al., 2013; Coolen et al., 2020a; Mavraki et al., 2021), supporting a high faunal diversity, potentially including non-indigenous and locally rare species (Degraer et al., 2020). Functionally, this AHS community is dominated by suspension feeders and thus acts as a biofilter (Slavik et al., 2019), redirecting organic matter from the water column towards the surrounding benthic community as detrital particulate organic matter, fuelling the benthic food web and the higher trophic levels that depend on it (Krone et al., 2017; Roa-Ureta et al., 2019; Ivanov et al., 2021). Consequently, OWF AHS communities are likely to have an overall facilitative effect on local secondary production and benthic mineralisation pathways (De Borger et al., 2021).

When working towards a fully decarbonised power system, it is indispensable to consider the (relatively local) effects of OWF AHSs on the marine ecosystem in the larger scheme of (global) climate change. Overall, increasing sea surface temperatures and decreasing surface water pH-levels have widespread effects on the survival, productivity and growth of marine organisms and the projected changes in ocean temperature and pH pose significant risks and vulnerabilities to the provision of marine ecosystem services (IPCC, 2018; Bindoff et al., 2019). Consequently, climate change is likely to affect both structural and functional aspects of marine ecosystems, through changes in species composition, behavioural and physiological ecology (i.a. reviewed in Hoegh-Guldberg et al., 2014). To guide informed offshore renewable energy industry and policy decisions, it is therefore essential to fully comprehend the reciprocal effects of the local introduction of OWFs in addition to global climate change on the coastal

ecosystem. To this end, this research aims to provide much needed in-depth knowledge on both the effects of the newly established OWF AHS communities on the marine ecosystem, and how this altered ecosystem will react to climate change.

Research on the individual impacts of temperature and ocean acidification has been conducted on a wide variety of marine species, but not often, as is the case in this study, in combination with each other (but see e.g. Freitas et al., 2017; Gu et al., 2019; Glon et al., 2019). Furthermore, these impacts are considered to be species-specific and with substantial variation within functional groups (Hoegh-Guldberg et al., 2014; Bindoff et al., 2019), impeding the prediction of climate change effects at the community level and the functional implications for the local ecosystem, including the delivery of ecosystem services (Pörtner and Farrell, 2008). The use of model species to predict the overlying ecosystem response is therefore a proven method, as their changes in abundance, survival, condition or distribution will affect the ecosystem as a whole (Verdelhos et al., 2015; Kotta et al., 2019; Van Colen et al., 2020).

Here, we report for the first time how the functional effects of OWFs on the marine environment can change due to global warming, ocean acidification and the combination of both. This work is based on ecophysiological measurements conducted on three model species, representing the vertical zonation of established AHS colonising fauna assemblages found on OWF turbines: the infralittoral blue mussel *Mytilus edulis*, the sublittoral tube-building amphipod *Jassa herdmani* and the lower sublittoral plumose anemone *Metridium senile* (respectively referred to as *Mytilus*, *Jassa* and *Metridium* individuals/experiments; Mavraki et al., 2020; Coolen et al., 2020b). The relative importance of these model species in the overall OWF AHS ecosystem, i.a. in terms of total densities, filtration capacity and competition dominance (Jak and Glorius, 2017; Coolen et al., 2020b), makes them ideally suited to assess functional implications at OWF AHS community level. In particular the model species' cumulative clearance effect on various suspended food particles could serve as an indicator for the (changes in) functioning of this relatively novel ecosystem in current and future climate conditions. To understand the drivers behind these changes, analogous experiments were set up over the course of three years, testing the effect of increased temperature and lowered pH on the ecophysiology of all three model species in a full factorial design. This knowledge was subsequently used to calculate a newly defined metric, the maximised cumulative clearance potential, and used as the basis for a first upscaling exercise going from a single species response to a higher level OWF community response. Additionally, the species-specific ecophysiological results of this study can directly feed into an ecological model to simulate and study the fluctuations in colonising fauna biomass in both current and future climate conditions, as well as help further understand the potential cascading effects on the surrounding environment (Voet et al., 2021) or beyond (Ivanov et al., 2021; De Borger et al., 2021). Such ecological models support informed decisions on the design and installation of offshore wind farms, for example with regards to the distance between individual wind turbines or the system's carrying capacity when looking into multifunctional co-use between OWFs and blue mussel mariculture (Voet et al., 2021).

This research combines data from mortality, respiration, clearance and growth experiments under acidified, warmed and combined climate change conditions. We hypothesised that ocean warming and acidification would interactively affect the survival and ecophysiology of *M. edulis*, *J. herdmani* and *M. senile* in a species-specific manner, hereby altering the maximised cumulative clearance potential of the dominantly suspension-feeding OWF AHS community under predicted climate change conditions.

2. Methodology

A methodology flowchart is presented in Supplementary Fig. 1.

2.1. Sampling and incubation

In summer 2017, 2018 and 2019, hard substrate fauna was collected from turbine D6 in the C-Power wind farm (51°33.04'N - 02°55.42'E), as

well as from an aquaculture pilot project approximately 10 km off the Belgian coast (51°11.02'N - 02°39.88'E). *M. edulis* was sampled by hauling an aquaculture longline on deck, while *Jassa herdmani* and *Metridium senile* were collected from the OWF turbine foundation by scientific divers at 7 m and 18 m depth, respectively. All samples were stored in aerated seawater and transported to the experimental facilities within 4 h.

All animals were randomly assigned to one of four experimental treatments. *Mytilus* individuals ($n_{TOT} = 800$) with an average length of 44.76 ± 0.42 mm (SE) were distributed across four identical aquaria ($100 \times 45 \times 70$ cm) equipped with a continuous flow-through mechanism with a total of approximately 400 L in circulation per system, allowing for homogenisation of the seawater. *Jassa* individuals ($n_{TOT} = 600$; length > 5 mm) were equally divided among a total of 12 cylindrical aquaria ($\varnothing 12$ cm x h 25 cm) equipped with a 1 mm mesh for the animals to attach to (Mavraki N., personal communication, 2018). *Metridium* individuals ($n_{TOT} = 480$) with an average pedal disc diameter of 24.13 ± 0.53 mm (SE) were divided among 12 replicate aquaria ($40 \times 20 \times 30$ cm). The *Jassa* and *Metridium* aquaria were hooked up to four independent continuous flow-through systems that allowed three aquaria per system to overflow into the same 2000-4000 L holding tank. All types of aquaria were aerated and filled with natural seawater at pre-set laboratory conditions, mimicking the seawater salinity, temperature and pH at the time of sampling (34 PSU, 20 °C and pH 7.96; LifeWatch Belgium, 2015).

Both temperature and pH of the seawater were manipulated individually across the aquaria, resulting in a fully crossed experiment with four different experimental treatments: a control treatment (CTRL: current temperature and pH), an ocean acidification treatment (OA: current temperature and lowered pH), an ocean warming treatment (OW: elevated temperature and current pH) and a combined climate change treatment (CC: combined elevated temperature and lowered pH).

After allowing the animals to acclimatise for 48 h under ambient conditions, seawater temperature was increased by 1 °C per day and pH was decreased by 0.1 pH unit per day for three days, resulting in seawater of +3 °C and/or -0.3 pH units in the corresponding treatments compared to the control settings. The level of manipulation was chosen in accordance with the IPCC RCP8.5 projections for ocean warming and acidification towards the end of this century (Hoegh-Guldberg et al., 2014). These conditions were maintained for 21 days in the *Jassa* experiment and 42 days in the *Mytilus* and *Metridium* experiments. Seawater temperature was regulated using TECO TK2000 heaters (*M. edulis*) or Aqua Medic Titan 8000 professional units (*J. herdmani* and *M. senile*). pH was manipulated through the controlled bubbling of 100% CO₂ in the OA and CC treatment tanks using the IKS AquaStar aquaristic computer system (*M. edulis*) or a personalised Fleuren&Nooijen JUMO microprocessor (*J. herdmani* and *M. senile*). Glass pH electrodes were calibrated weekly using Hanna Instruments™ NIST Reference Buffer Solutions (4.01 and 7.01) and all temperature and pH data was logged throughout the experiment (Appendix A - Appendix C).

Tank water was sampled weekly and filtered through GF/C papers to determine Total Alkalinity (TA) using a CONTROS HydroFIA™TA alkalinity system. The carbonate chemistry of the seawater was calculated using CO₂SYS software (Pierrot et al., 2006), using the thermodynamic constants of Mehrbach et al. (1973). Animals were fed twice a week by adding 5 mL Shellfish Diet 1800® (Instant Algae® mix by Reed Mariculture Inc.), 20 mL live *Artemia* sp. nauplii solution or 50 mL zooplankton mix (RUTO frozen fishfood®) to the aquaria of *M. edulis*, *J. herdmani* and *M. senile*, respectively.

2.2. Survival and ecophysiological parameters

Survival in each experimental treatment was monitored every two to three days throughout the experiment using a dedicated batch of individually numbered organisms (*M. edulis* and *M. senile*) or using the total population in the aquaria (*J. herdmani*). Dead animals were routinely removed from the aquaria. The overall high mortality of *Jassa* individuals limited the duration of this experiment to three weeks, as opposed to the six-week *Mytilus* and *Metridium* experiments.

The ecophysiological parameters measured for all three model species were respiration rate (RR) and clearance rate (CR). Volumetric growth was measured for *M. edulis* and *M. senile* (*J. herdmani* was excluded because it moults). To measure RR and CR, triplicated individual closed-core incubations were set up in each experimental treatment. Each incubation core held one individual, along with manipulated seawater from the respective treatment, and was kept at the correct temperature throughout the incubations. Seawater inside was kept in motion to ensure an evenly mixed water column using either stirring discs (*M. edulis* and *M. senile*) or a shaking table (*J. herdmani*). The incubation core volume was corrected with the biovolume (mL) of *Mytilus* and *Metridium* individuals, measured by water displacement in a 500 ± 2 mL graduated cylinder, while the biovolume of *Jassa* individuals was considered negligible.

Survival (%) was calculated as the proportionate survival per experimental treatment, with 100% survival at the start (day 0), according to Eq. (1):

$$\text{Survival (\%)} = \frac{N_i}{N_0} \times 100 \quad (1)$$

with N_0 and N_i the number of living individuals in the dedicated batch of organisms in each experimental treatment at day 0 and day i of the experiment, respectively. The number of individuals in each experimental treatment dedicated to the monitoring of survival was $N_0 = 75$ for *M. edulis*, $N_0 = 132$ for *J. herdmani* and $N_0 = 58$ for *M. senile*.

Respiration rates (RR) were based on the decrease in dissolved oxygen during the closed-core incubations. Seawater oxygen concentration ($\mu\text{mol L}^{-1}$) inside the incubation cores was measured continuously (*M. senile* and *J. herdmani*) or discretely (*M. edulis*) using PyroScience™ robust optical oxygen probes (*M. edulis* and *M. senile*) or sensor spots (*J. herdmani*) with REDFLASH-technology connected to a PyroScience™ FireSting O₂ logger. The closed-core respiration measurements were done weekly in a volume of 1.5 L, 8.15 L or 5 mL and lasted 3 h, 2.5 h or 1 h for *M. edulis*, *M. senile* and *J. herdmani*, respectively. Respiration rates were calculated using Eq. (2) (*M. edulis*) or Eq. (3) (*J. herdmani* and *M. senile*):

$$\text{RR } (\mu\text{mol g}^{-1} \text{ h}^{-1}) = \frac{V(C_0 - C_1)}{g(t_1 - t_0)} \quad (2)$$

$$\text{RR } (\mu\text{mol g}^{-1} \text{ h}^{-1}) = \frac{V}{g} \times \text{regression slope} \quad (3)$$

where V is the seawater volume (L) of the incubation core after correction for the biovolume of the organism, C_0 and C_1 are the respective dissolved oxygen concentrations ($\mu\text{mol L}^{-1}$) at the start and end time t_0 and t_1 (h) of measurement, respectively, g is the dry weight (g) of the animal's soft tissue and the regression slope is that of the linear regression through continuous oxygen measurements. A separate, simultaneous incubation for each experimental treatment was used to correct for background changes in dissolved oxygen, e.g. due to bacterial respiration or phytoplankton photosynthesis.

Clearance rates (CR), as a measure of the volume of water cleared by the organism, were calculated as the decline in algal cells, *Artemia* nauplii or mixed zooplankton over time in the incubation cores with *M. edulis*, *J. herdmani* and *M. senile*, respectively. To do this, incubation cores with and without organisms was set up in each experimental treatment and a known quantity of the respective food item was added to each core. The CR incubations were done in week 3 and 6 of the *M. edulis* experiment and weekly in the *J. herdmani* and *M. senile* experiments. After an initial mixing period of 30 min, discrete water samples were taken every 50 min throughout the 150-min incubation with *M. edulis* and every 30 min throughout the 90-min incubation with *J. herdmani* and *M. senile*.

Algal cell concentrations were determined using a BECKMAN Coulter Multisizer (100 μm aperture) and the number of *Artemia* nauplii or assorted

zooplankton was determined using a HydroptiC zooSCAN. Clearance rates were calculated according to Eq. (4), following Coughlan (1969):

$$CR \text{ (L g}^{-1} \text{ h}^{-1}) = \frac{V}{g \times t} \left(\ln \frac{C_1}{C_0} - \ln \frac{C_1'}{C_0'} \right) \quad (4)$$

where V is the seawater volume of the incubation core (L), corrected for the biovolume of the organism; g is the dry weight (g) of the animal; t is the duration of the incubation (h); C_0 is the food concentration at the start of the incubation, C_1 is the concentration at the end, while C_0' and C_1' are the food concentrations at the start and end of the empty control incubation, respectively. For every calculation, the condition of linearity of $\ln \frac{C_0}{C_1}$ in Eq. (4) was confirmed (Riisgård, 2001).

Volumetric growth (%) was calculated using weekly measurements of individually numbered *Mytilus* ($n_{\text{tot}} = 72$) and *Metridium* ($n_{\text{tot}} = 48$) individuals in all four experimental treatments. *Mytilus* individuals were measured weekly in three dimensions (length x width x height) to calculate the volume of an ellipsoid, approximating the shape of the closed mussel shell (Eq. (5); Fig. 1). The volume of an ellipsoid can be described as:

$$V \text{ (cm}^3\text{)} = \frac{4}{3} \pi \times a \times b \times c \quad (5)$$

with a, b and c (cm) the three axes of the ellipsoid and the double axes 2a, 2b and 2c (cm) the length, width and height of the closed mussel shell, respectively (Fig. 1). The growth of *Metridium* individuals was calculated by measuring the displaced water of the animal as a proxy for its biovolume (mL). Volumetric growth was expressed as percentage in- or decrease in ellipsoid volume (cm³, *M. edulis*) and biovolume (mL, *M. senile*) compared to that at the start of the experiment (Week 0).

2.3. Maximised cumulative clearance potential

The results of this study were combined with published work (Table 1) to estimate the 'maximised cumulative clearance potential' of the AHS epifauna community colonising an OWF monopile foundation in the Belgian part of the North Sea (BPNS). Using the mean individual biomass (gDW ind⁻¹), total density (ind m⁻²) and total surface area (m²) occupied by *M. edulis*, *J. herdmanni* and *M. senile*, the estimated total biomass (gDW) present on a monopile foundation was calculated. These species-specific total biomasses were multiplied with the species-specific mean clearance rates (L gDW⁻¹ h⁻¹) and corrected with the respective proportional survival (%) and the estimated fraction of feeding individuals (%), since thumbed *J. herdmanni* males do not feed excessively (estimated to make up ± 16% of individuals in the field; Beermann and Franke, 2012; Beermann and Purz, 2013). These results were then amended according to the CTRL and CC treatments to estimate the species-specific total volume of seawater potentially cleared around a monopile foundation per day (m³ d⁻¹) in current

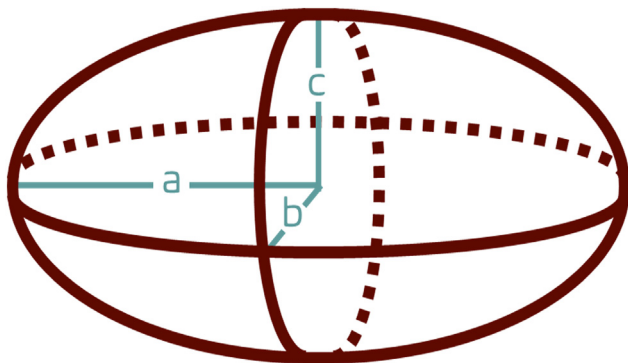


Fig. 1. Ellipsoid (with three axes a, b and c) as an approximated volume of a closed mussel shell.

Table 1

Data used for the calculation of estimated cumulative clearance potential of the artificial hard substrate fauna community inhabiting an OWF monopile foundation in the Belgian part of the North Sea (BPNS): mean individual biomass (gDW ind⁻¹), total densities (ind m⁻²), total surface area (m²) per species and mean diameter of monopile foundation (m).

	Value	Reference
Mean biomass (gDW ind ⁻¹)		
<i>Mytilus edulis</i>	0.785	This study
<i>Jassa herdmanni</i>	0.002	This study
<i>Metridium senile</i>	1.651	This study
Total density (ind m ⁻²)		
<i>Mytilus edulis</i>	1843	Mavraki et al. (2020)
<i>Jassa herdmanni</i>	24,339	Mavraki et al. (2020)
<i>Metridium senile</i>	480	Unpublished personal data
Total surface area (m ²)		
<i>Mytilus edulis</i>	192	Rumes et al. (2013), as cited in Mavraki et al. (2020)
<i>Jassa herdmanni</i>	384	Rumes et al. (2013), as cited in Mavraki et al. (2020)
<i>Metridium senile</i>	220	Unpublished personal data
Mean diameter (m)		
Monopile foundation	7.25	Degraer et al. (2016)

and future climate (CTRL and CC, respectively) and subsequently summed, which was justified by this region's well-mixed water column (Van Leeuwen et al., 2015). Monopile foundation dimensions were used to convert these calculated total volumes into a more perceivable measure, the *maximised cumulative clearance potential*: the estimated radial distance around the monopile foundation (m) equal to the width of a cylindrical sleeve with a volume equivalent to the seawater volume being cleared daily due to the presence of the AHS epifaunal community (Fig. 2).

2.4. Statistical analysis

A Cox proportional hazards regression model was fitted for mortality events in each species. The effect of the manipulated experimental

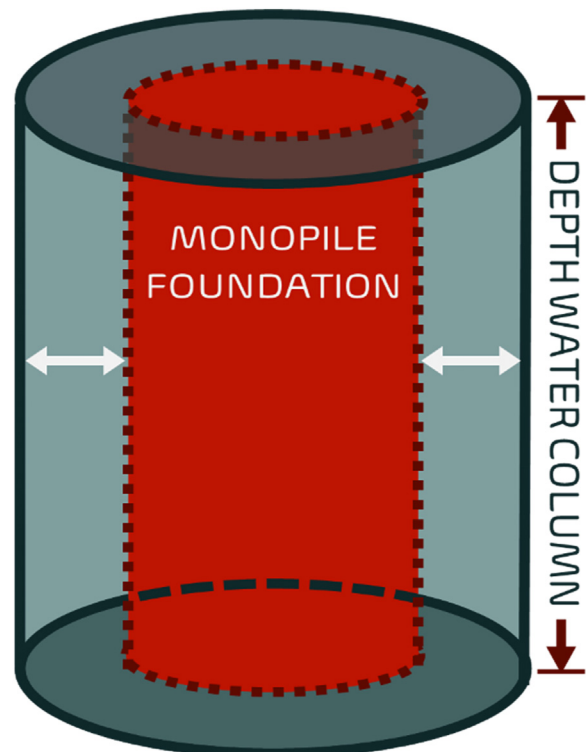


Fig. 2. Schematic representation of the cumulative clearance potential as a cylindrical sleeve of seawater around a monopile foundation, with width = radial distance (white arrows) and height = depth of the water column.

treatments on survival, compared to that in CTRL, was evaluated using hazard ratio (HR) with 95% confidence intervals. Additionally, a pairwise proportion test with Bonferroni correction was used to test for differences in survival between all four treatments at the end of the experiment.

The effects of temperature (current or elevated) and pH (current or lowered) on the ecophysiological parameters were investigated using a series of linear mixed effects models, where incubation core, individual organism identity and/or time (weekly incubations) was added as a random factor to the models. If none of the random factors significantly contributed to explained left-over variance, a linear regression model was fitted. Significance of the two-way interaction 'temperature x pH' and post-hoc pairwise comparison of the group means was used to identify possible additive, synergistic, antagonistic or potentiating combination effects of increased temperature and lowered pH (Table 2). For each parameter, normality of the residuals and model assumptions were checked and data was transformed if necessary. Appropriate Gaussian or Gamma error distributions were used and model selection was based on the parametric bootstrap and Kenward Roger methods for mixed model comparison (Halekoh and Højsgaard, 2014).

Analyses were conducted using R v3.6.1 with RStudio v1.4.1106 (RStudio Team, 2016; R Core Team, 2019), Cox survivorship models were fitted using the R packages *survival* (Therneau, 2021) and *coxed* (Kropko and Harden, 2020), linear regression models were fitted using the *stats* package (R Core Team, 2019), linear mixed effects models were built using the R package *lme4* (Bates et al., 2015) and the conditional R² (R²c) for linear mixed effects models (to be interpreted as the variance explained by the entire model, including both fixed and random effects) was calculated using the *MuMIn* package (Barton, 2020).

Species-specific mean clearance rates were summed to estimate the maximised cumulative clearance potential of the OWF AHS community and an appropriate cumulative standard error on this estimate was calculated by taking the square root of the quadratically summed standard deviations (i.e. the summed variances), considering the species-specific mean clearance rates are derived from independent experimental set-ups. The estimated cumulative clearance potential was compared between both current and future climate (CTRL and CC, respectively) using an ANOVA approach for summarised data in the R package *rpschi* (Okumura, 2012).

3. Results

3.1. Experimental conditions

Temperature (\pm SE) in the warmed treatments (OW and CC) ranged between 23.00 ± 0.05 °C and 23.20 ± 0.05 °C, on average 3.02 ± 0.05 °C warmer than in CTRL. The CTRL seawater pH (\pm SE) ranged between 7.91 ± 0.00 and 7.96 ± 0.01 , and was reduced on average by 0.29 ± 0.01 in OA and by 0.30 ± 0.01 in CC (Table 3, Appendix A - Appendix B). Small differences in salinity measured during the experiments were caused by the random distribution of barrelled natural seawater across the experimental treatments.

Throughout all three experiments, carbonate chemistry parameters varied as a result of the imposed temperature and pH conditions (Table 4). The average aragonite and calcite saturation states of the seawater (\pm SE) ranged, respectively, between 0.82 ± 0.08 and 1.64 ± 0.04 in the acidified treatments and between 1.66 ± 0.05 and 3.03 ± 0.11 in the non-acidified treatments (Table 4).

Table 2
Possible combination effects.

Combination	Definition	Example
Additive	Combined effect is sum of individual effects	$X + X = 2X$
Synergistic	Combined effect exceeds sum of individual effects	$X + X > 2X$
Antagonistic	Combination causes decrease of individual effects	$X + X < 2X$
Potentiating	Combination with otherwise inert effect enhances other's individual effect	$0 + X > X$

Table 3

Average seawater temperature (°C), pH and salinity (PSU) of four experimental treatments throughout *Mytilus edulis*, *Jassa herdmani* and *Metridium senile* experiments (\pm SE).

	CTRL	OA	OW	CC
Temperature (°C)				
<i>Mytilus edulis</i>	20.02 ± 0.05	19.99 ± 0.12	23.15 ± 0.10	23.13 ± 0.13
<i>Jassa herdmani</i>	20.08 ± 0.06	19.98 ± 0.02	23.20 ± 0.05	23.04 ± 0.03
<i>Metridium senile</i>	20.14 ± 0.05	20.17 ± 0.08	23.10 ± 0.08	23.00 ± 0.05
pH				
<i>Mytilus edulis</i>	7.96 ± 0.01	7.65 ± 0.01	7.97 ± 0.01	7.65 ± 0.00
<i>Jassa herdmani</i>	7.92 ± 0.00	7.63 ± 0.00	7.92 ± 0.01	7.63 ± 0.00
<i>Metridium senile</i>	7.91 ± 0.00	7.63 ± 0.01	7.92 ± 0.01	7.62 ± 0.01
Salinity (PSU)				
<i>Mytilus edulis</i>	32.9 ± 0.2	32.4 ± 0.2	33.8 ± 0.2	33.0 ± 0.2
<i>Jassa herdmani</i>	32.1 ± 0.1	33.2 ± 0.0	33.9 ± 0.1	32.9 ± 0.1
<i>Metridium senile</i>	32.5 ± 0.1	35.2 ± 0.6	33.6 ± 0.1	33.4 ± 0.1

3.2. Survival and ecophysiological parameters

The survival of *M. edulis* at the end of the experiment was significantly lower in the CC treatment (66.6%) compared to the CTRL treatment (97.3%) and OW treatment (89.3%) ($p_{adj} < 0.01$; Fig. 3). Both acidified treatments had a significant hazard ratio $HR > 1$, indicating the magnitude of increased risk of mortality over time compared to CTRL ($HR_{OA} = 6.47$, $HR_{CC} = 15.23$; $p < 0.05$; Table 5). In *J. herdmani*, survival at the end of the experiment was significantly lower in all manipulated treatments ($< 21.2\%$) compared to CTRL (40.2%; $p_{adj} < 0.01$) and the survival in the CC treatment was significantly lower than in the single OA and OW treatments ($p_{adj} < 0.05$; Fig. 3). Hazard ratios of *J. herdmani* were significantly $HR > 1$ across all manipulated treatments compared to CTRL ($HR_{OA} = 1.80$, $HR_{OW} = 1.58$ and $HR_{CC} = 2.80$; $p < 0.01$; Table 5). In *M. senile*, only the survival measured at the end of the

Table 4

Average seawater carbonate chemistry of four experimental treatments throughout *Mytilus edulis*, *Jassa herdmani* and *Metridium senile* experiments (\pm SE): Total Alkalinity (TA; $\mu\text{mol kg}^{-1}$), partial pressure of CO₂ (pCO₂; μatm), total inorganic carbon concentration (C_T; $\mu\text{mol kg}^{-1}$), concentration of bicarbonate and carbonate ion (HCO₃⁻ and CO₃²⁻; $\mu\text{mol kg}^{-1}$) and saturation state of the seawater with respect to aragonite (Ω_A) and calcite (Ω_C).

	CTRL	OA	OW	CC
TA ($\mu\text{mol kg}^{-1}$)				
<i>Mytilus edulis</i>	2107 ± 101	1985 ± 114	2113 ± 110	2038 ± 130
<i>Jassa herdmani</i>	2302 ± 176	2378 ± 221	2357 ± 178	2232 ± 167
<i>Metridium senile</i>	2305 ± 75	2530 ± 68	2375 ± 74	2381 ± 42
pCO ₂ (μatm)				
<i>Mytilus edulis</i>	652 ± 19	1361 ± 52	650 ± 16	1420 ± 60
<i>Jassa herdmani</i>	798 ± 61	1689 ± 142	827 ± 58	1646 ± 126
<i>Metridium senile</i>	825 ± 30	1786 ± 65	831 ± 35	1802 ± 29
C _T ($\mu\text{mol kg}^{-1}$)				
<i>Mytilus edulis</i>	1967 ± 92	1951 ± 111	1951 ± 97	1991 ± 125
<i>Jassa herdmani</i>	2174 ± 169	2345 ± 220	2203 ± 169	2191 ± 166
<i>Metridium senile</i>	2180 ± 73	2490 ± 68	2221 ± 71	2342 ± 40
HCO ₃ ⁻ ($\mu\text{mol kg}^{-1}$)				
<i>Mytilus edulis</i>	1838 ± 83	1854 ± 104	1808 ± 85	1888 ± 117
<i>Jassa herdmani</i>	2041 ± 159	2228 ± 209	2054 ± 157	2079 ± 158
<i>Metridium senile</i>	2048 ± 69	2364 ± 65	2072 ± 66	2222 ± 38
CO ₃ ²⁻ ($\mu\text{mol kg}^{-1}$)				
<i>Mytilus edulis</i>	108 ± 9	52 ± 5	123 ± 12	60 ± 6
<i>Jassa herdmani</i>	107 ± 9	62 ± 6	124 ± 10	62 ± 5
<i>Metridium senile</i>	105 ± 3	69 ± 2	125 ± 4	66 ± 2
Ω_A				
<i>Mytilus edulis</i>	1.70 ± 0.13	0.82 ± 0.08	1.95 ± 0.18	0.96 ± 0.09
<i>Jassa herdmani</i>	1.69 ± 0.14	0.97 ± 0.10	1.97 ± 0.16	0.99 ± 0.07
<i>Metridium senile</i>	1.66 ± 0.05	1.07 ± 0.02	1.98 ± 0.07	1.04 ± 0.03
Ω_C				
<i>Mytilus edulis</i>	2.63 ± 0.16	1.27 ± 0.09	2.97 ± 0.21	1.46 ± 0.11
<i>Jassa herdmani</i>	2.62 ± 0.22	1.49 ± 0.15	3.01 ± 0.25	1.52 ± 0.11
<i>Metridium senile</i>	2.57 ± 0.08	1.64 ± 0.04	3.03 ± 0.11	1.59 ± 0.05

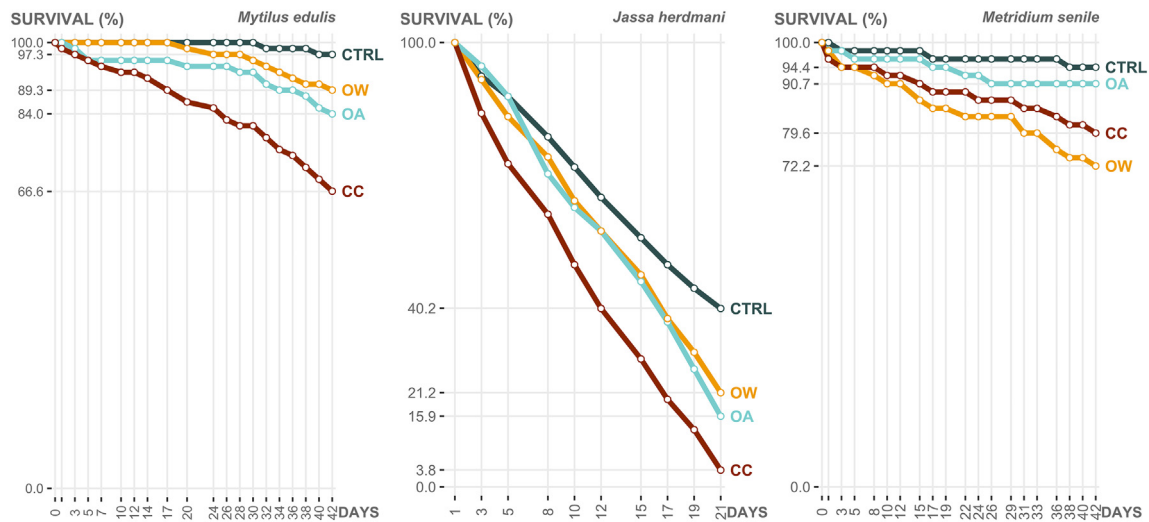


Fig. 3. Proportional survival (%) of *Mytilus edulis* (left), *Jassa herdmani* (middle) and *Metridium senile* (right) throughout the six- and three-week experiments in four experimental treatments (CTRL: control, OA: ocean acidification, OW: ocean warming and CC: climate change).

experiment in the OW treatment (72.2%) was significantly lower than that in the CTRL treatment (94.4%) ($p_{\text{adj}} = 0.027$; Fig. 3) and both warmed treatments had significant HR > 1 compared to CTRL ($\text{HR}_{\text{OW}} = 5.62$ and $\text{HR}_{\text{CC}} = 3.97$; $p < 0.05$; Table 5).

In *M. edulis*, there was a significant additive effect of both elevated temperature and decreased pH on respiration rate ($p < 0.01$; Table 6), with the highest mean respiration rate (\pm SE) in CC ($69.68 \pm 0.71 \mu\text{mol O}_2 \text{ g}^{-1}\text{DW}$; Fig. 4). In the *Jassa* experiment, lowered pH significantly increased the respiration rate ($p < 0.001$), while elevated temperature added a potentiating combination effect on this response ($p = 0.002$; Table 6): the highest mean respiration rate (\pm SE) was measured in CC ($55.76 \pm 22.63 \mu\text{mol O}_2 \text{ g}^{-1}\text{DW}$; Fig. 4). Elevated temperature significantly increased respiration rate in *M. senile* ($p < 0.001$; Table 6) independently of pH, with the highest mean respiration rate (\pm SE) measured in OW ($56.71 \pm 6.72 \mu\text{mol O}_2 \text{ g}^{-1}\text{DW h}^{-1}$; Fig. 4).

In both *M. edulis* and *J. herdmani*, there was a significant additive effect of elevated temperature and lowered pH on clearance rates ($p < 0.001$; Table 6), with the highest mean clearance rate (\pm SE) measured in CC (*M. edulis*: $3.07 \pm 0.22 \text{ L g}^{-1}\text{DW h}^{-1}$ and *J. herdmani*: $38.54 \pm 3.99 \text{ L g}^{-1}\text{DW h}^{-1}$; Fig. 5). In contrast, clearance rate significantly increased with lowered pH and significantly decreased with elevated temperature in

Table 5

Hazard ratios of Cox proportional hazard regression models for three manipulated experimental treatments compared to CTRL: OA (ocean acidification), OW (ocean warming) and CC (climate change). Significance indicated in bold. [HR = hazard ratio over CTRL, CI_{95} = 95% HR confidence interval].

	HR	CI_{95}	p-value
<i>Mytilus edulis</i>			
CTRL			
OA	6.47	1.45–28.91	0.014
OW	4.16	0.88–19.58	0.071
CC	15.23	3.61–64.30	<0.001
<i>Jassa herdmani</i>			
CTRL			
OA	1.80	1.35–2.40	<0.001
OW	1.58	1.18–2.12	0.002
CC	2.80	2.11–3.72	<0.001
<i>Metridium senile</i>			
CTRL			
OA	1.72	0.41–7.19	0.459
OW	5.62	1.63–19.43	0.006
CC	3.97	1.11–14.24	0.034

the *Metridium* experiment, causing a significant antagonistic effect when combined in the CC treatment ($p < 0.01$; Table 6). The highest mean clearance rate (\pm SE) was measured in OA ($4.48 \pm 0.26 \text{ L g}^{-1}\text{DW h}^{-1}$; Fig. 5).

A significant positive effect of elevated temperature and a significant negative effect of lowered pH on volumetric growth (\pm SE) in the *Mytilus* experiment ($p < 0.001$; Table 6) caused the average biovolume of *M. edulis* (\pm SE; $7.24 \pm 0.18 \text{ cm}^3$ at the start) to increase the most in OW ($4.27 \pm 0.28\%$) and the least in OA ($0.62 \pm 0.11\%$) after six weeks (Fig. 6). An opposite significant antagonistic effect was recorded for volumetric growth (\pm SE) in the *Metridium* experiment ($p = 0.001$ Table 6), where the average biovolume (\pm SE; $21.46 \pm 0.53 \text{ cm}^3$ at the start) increased the most in OA ($37.48 \pm 4.40\%$) and decreased in OW ($-15.92 \pm 1.65\%$; Fig. 6).

3.3. Maximised cumulative clearance potential

The mean clearance rate ($\text{L g}^{-1}\text{DW h}^{-1}$) of *M. edulis*, *J. herdmani* and *M. senile* was experimentally quantified in a current (CTRL) and future (CC) climate scenario and amassed to an estimated cumulative mean volume of seawater

Table 6

Conditional R^2 (R^2_{c} ; for entire model including fixed and random effects) and structure of final ecophysiological linear mixed effects and linear regression models with significance of fixed effects Temperature (TEMP), pH (PH) and two-way interaction (TEMP x PH), and with identity of random effects, including random intercept (format = 1|random) and potential random slope (format = 1 + fixed|random). Significance indicated in bold. [WEEK = experimental week, CORE = incubation core, INDIV = individual organism, NA = not applicable].

	R^2_{c}	Fixed effects			Random effects
		TEMP	PH	TEMP x PH	
Respiration rate [$\mu\text{mol O}_2 \text{ g}^{-1}\text{DW h}^{-1}$]					
<i>Mytilus edulis</i>	0.58	$p < 0.001$	$p = 0.002$	0.265	1 CORE
<i>Jassa herdmani</i>	0.70	0.920	$p < 0.001$	$p = 0.002$	1 + TEMP WEEK
<i>Metridium senile</i>	0.40	$p < 0.001$	0.290	0.193	1 CORE
Clearance rate [$\text{L g}^{-1}\text{DW h}^{-1}$]					
<i>Mytilus edulis</i>	0.73	$p < 0.001$	$p < 0.001$	0.742	1 WEEK
<i>Jassa herdmani</i>	0.71	$p < 0.001$	$p < 0.001$	0.235	1 WEEK
<i>Metridium senile</i>	0.49	$p < 0.001$	$p < 0.001$	$p = 0.007$	NA
Volumetric growth [%]					
<i>Mytilus edulis</i>	0.82	$p < 0.001$	$p < 0.001$	0.451	1 + PH WEEK 1 INDIV
<i>Metridium senile</i>	0.61	0.166	0.237	$p = 0.001$	1 + TEMP WEEK 1 INDIV

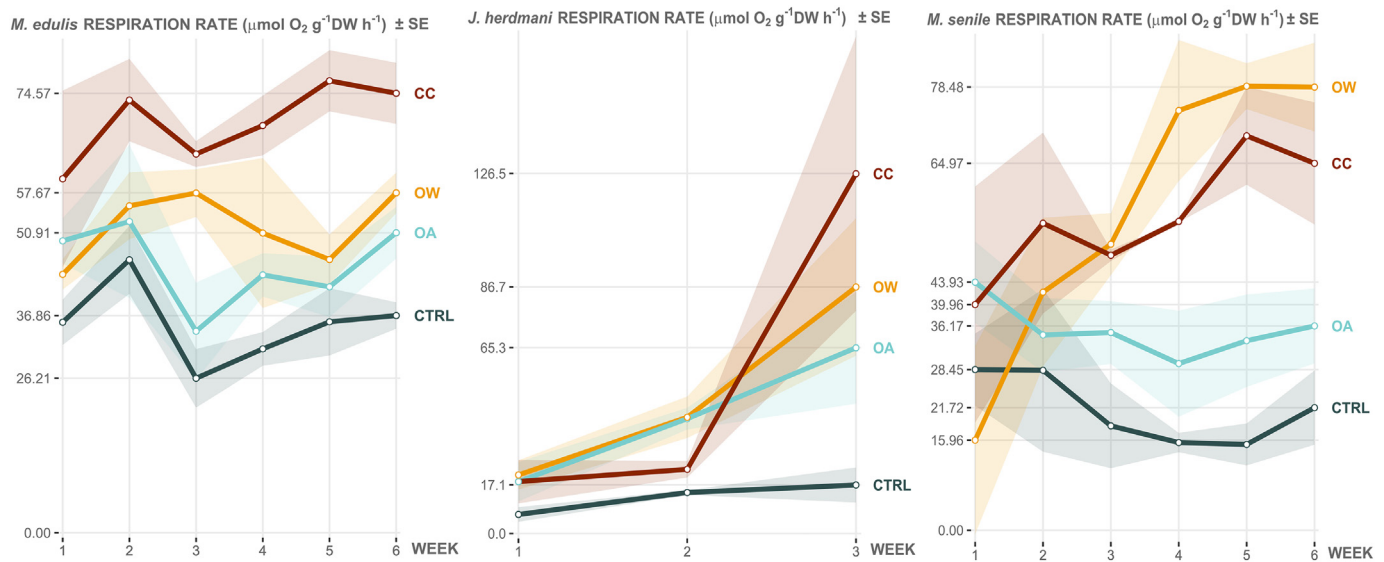


Fig. 4. Mean respiration rate ($\mu\text{mol O}_2 \text{ g}^{-1}\text{DW h}^{-1} \pm \text{SE shaded area}$) of *Mytilus edulis* (left), *Jassa herdmani* (middle) and *Metridium senile* (right) throughout the six- and three-week experiments in four experimental treatments (CTRL: control, OA: ocean acidification, OW: ocean warming and CC: climate change). Note difference in scale.

($\pm \text{SD}$) cleared by the OWF AHS community per day of $18,929 \pm 4048 \text{ m}^3$ in CTRL and $21,972 \pm 3643 \text{ m}^3$ in CC, a significant increase of 16.07% (ANOVA; $F_{1,64} = 10.31, p = 0.002$). This maximised cumulative clearance potential ($\pm \text{SD}$) of *M. edulis*, *J. herdmani* and *M. senile* corresponds to a distance (m) from the monopile foundation of $12.69 \pm 4.79 \text{ m}$ in CTRL, increasing to $13.86 \pm 4.47 \text{ m}$ in CC ($F_{1,64} = 1.05, p = 0.31$), to which seawater is potentially fully cleared from suspended food particles.

4. Discussion

Temperature is one of the most important limiting factors in geographical distribution of marine ectotherms, influencing various physiological processes and biological performance, while ocean acidification might further narrow this species-specific thermal window (Pörtner and Farrell, 2008; Verdelhos et al., 2015). Exposure to either thermal stress, acidification or the combination of both, could therefore push aquatic organisms beyond their viable limits if acclimatisation or adaptive mechanisms fail to maintain whole-organism performance (Pörtner and Farrell, 2008;

Pörtner, 2012). As the offshore wind industry expands into the future, and since climate change will continue to impact the associated AHS communities, empirical studies are needed to integrate the effects of climate change and OWFs, as well as assess the current and future cascading effects of OWFs on the marine ecosystem. This study examined three model species representing a typical OWF AHS colonising community, the blue mussel *M. edulis*, the tube-building amphipod *Jassa herdmani* and the plumose anemone *Metridium senile*, and results show a species-specific survival and ecophysiological response to ocean warming and acidification, with various combination effects of both stressors. Additionally, such a colonising community was found to have a substantial impact on the local environment through its cumulative clearance potential, which was estimated to further enlarge ($\pm 16\%$) under projected future marine climate conditions.

Metabolic responses to temperature and pH stress are known to vary between species, most likely due to variable up- and downregulating metabolic mechanisms used by marine organisms attempting to maintain energy homeostasis and manage the short-term energy supply from i.a. lipids and glycogen in storage tissues (Sokolova et al., 2012; Liao et al.,

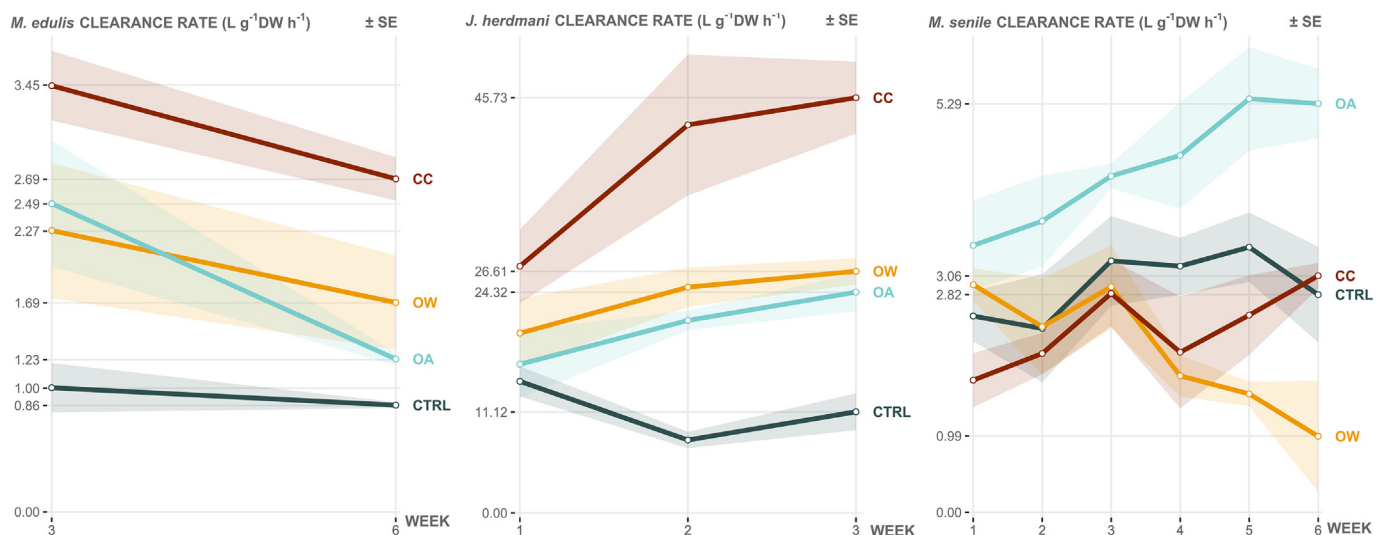


Fig. 5. Mean clearance rate ($\text{L g}^{-1}\text{DW h}^{-1} \pm \text{SE shaded area}$) of *Mytilus edulis* (left), *Jassa herdmani* (middle) and *Metridium senile* (right) throughout the six- and three-week experiments in four experimental treatments (CTRL: control, OA: ocean acidification, OW: ocean warming and CC: climate change). Note difference in scale.

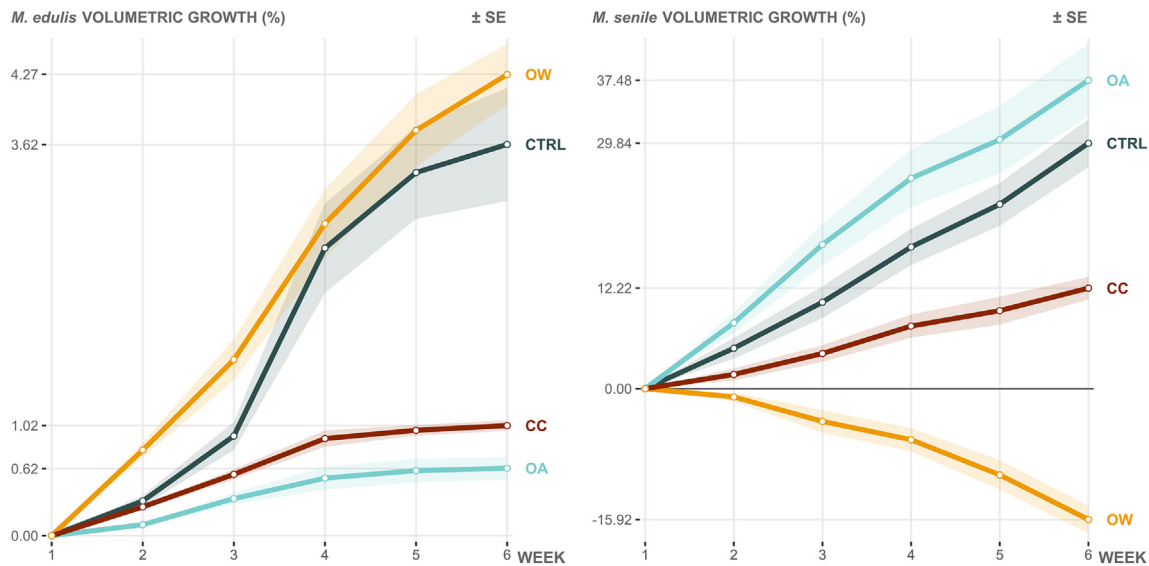


Fig. 6. Mean volumetric growth (% \pm SE shaded area) of *Mytilus edulis* (left) and *Metridium senile* (right) throughout the six-week experiments in four experimental treatments (CTRL: control, OA: ocean acidification, OW: ocean warming and CC: climate change). Note difference in scale.

2019). However, aerobic respiration rate, as a proxy for metabolic rate, unequivocally increased in all three model species in all manipulated treatments in this study. Such a boost in metabolism presumably comes at a substantial cost and is therefore unlikely to be sustainable long-term, as reflected in the reduced survival and growth rates across the investigated species. Despite the overall increased mortality and suppressed growth under predicted climate change conditions (i.e. combined ocean warming and acidification), single stressor effects varied between the model species and provide mechanistic insight into the observed response to climate change.

In *M. edulis*, lowered pH was detrimental for growth, similar to what was described by e.g. Berge et al. (2006), Bechmann et al. (2011) and Kong et al. (2019). Ocean acidification most likely affects bivalve growth through its impact on the carbonate saturation state of the seawater, which approached the saturation equilibrium ($\Omega = 1$) or even shifted towards an unfavourable equilibrium ($\Omega < 1$) in the acidified treatments in this study. This saturation state is directly linked to the availability of carbonate minerals and the ability of the organisms to biomineralize (Fitzer et al., 2015). Additionally, Fitzer et al. (2015) recorded a reduced impact of lowered pH on the material properties of *M. edulis* shells when combined with a higher temperature, identical to what was observed in the growth measurements in this study. In contrast, *M. senile* individuals in the ocean warming treatment effectively shrank in size, similar to what was observed for Actinaria (sea anemones) in times of temperature or starvation stress by Sebens (1980) and Chomsky et al. (2004). Most likely, this is caused by the anemone's inability to balance energy input and metabolic requirements. Indeed, biosynthetic activities in *M. senile* are suppressed in higher temperatures, with a significant effect on mortality and a lethal temperature for 50% (LT50) over 40 days reported at 24 °C (Walsh and Somero, 1981; Glon et al., 2019), corroborating the threefold increase in respiration rate of *M. senile* in this study's ocean warming treatment. However, an apparent insensitivity to lowered pH levels negated this effect in the combined climate change treatment, further substantiating the hypothesis that 'sea anemones may thrive in a high CO₂ world' (Suggett et al., 2012). Nevertheless, the increased clearance rates measured in the ocean acidification treatment suggest that a higher food intake is needed to support altered physiological needs and homeostasis under low pH conditions. Furthermore, feeding in *M. edulis* and *M. senile* is size-dependent (Anthony, 1997; Jacobs et al., 2015). Consequently, the relatively large size of *Mytilus* and *Metridium* individuals in the ocean warming and acidification treatments, respectively (see effect of temperature on growth), contributed to the observed changes in clearance rate (and thus food uptake) in support of the switch from a physiologically stable

state to an activated metabolic state under climate change conditions (Sokolova et al., 2012; Liao et al., 2019).

Overall, in this study, *M. edulis* and *J. herdmani* generally exhibited additive responses to elevated temperature and lowered pH. In contrast, *M. senile* most often showed an antagonistic response to temperature and pH manipulations, being inhibited by an elevated temperature and benefiting from a lower pH environment. In addition to the variable mortality of all three studied species across climate treatments and the challenge of producing these sound, replicated experimental data, the species-specific physiological responses and varying complexity of certain life traits complicate the quantification of the net ecological effect at the community level, exacerbating straightforward predictions on how the OWF AHS community might react to coastal climate change. Relatively simple calculations such as the maximised cumulative clearance potential can therefore act as a more perceivable, clear-cut upscaling assessment of the community effect on the surrounding ecosystem. In the current climate, the maximised cumulative clearance potential of the studied AHS community reached roughly 12.7 m around the OWF turbine, corresponding to a 'cleared' volume of ± 7.5 Olympic swimming pools every day and increasing up to 13.9 m or ± 9 Olympic swimming pools daily under climate change conditions. Through such a measurable effect on the water clearance, climate change and the increasing numbers of OWF installations in the North Sea could collectively affect the primary producer standing stock and zooplankton biomass in the vicinity of the OWFs (Boon et al., 2018; Mavraki et al., 2020) and beyond (Slavik et al., 2019). Moreover, such an effect would likely also increase the organic matter flux to the sediment in- and outside the OWF perimeters (Ivanov et al., 2021) and could alter local phytoplankton concentrations, fundamentally important for the OWF's ecological balance (Adhikary et al., 2021). In general, the predicted changes in OWF AHS community structure and functioning, and their spill-over effect beyond the turbine foundation and beyond the OWF perimeters, will impact the OWF's artificial reef effect and the interconnected (supporting) ecosystem services (Leadley et al., 2014; Causon and Gill, 2018; De Borger et al., 2021).

5. Conclusion

In conclusion, our results show a species-specific ecophysiological response of all three OWF AHS colonising model species to predicted changes in seawater temperature and pH, illustrating how localised impacts related to OWFs and global climate change can collectively induce larger-scale changes in the associated ecosystem functioning, which

governs the services provided by these marine ecosystems (Degraer et al., 2020). This should be of major concern, as these regulating and supporting ecosystem services, including their stability through time and space, underpin the fulfilment of current and future human population demands (Hoegh-Guldberg et al., 2014; Čosić-Flajsig et al., 2020). Data and results as presented in this study are a vital source of information for ecosystem-based ecological modelling, able to help industry and policy reach consensus on practical details concerning the design and installation of OWFs, while keeping in mind the impact on the surrounding ecosystem in both the present and future climate scenarios. Further understanding of interactive local and broad-scale environmental changes, especially on an ecosystem-level and/or in the long-term (including adaptation potential of the faunal communities), as well as how these environmental changes interact with other pressures on the marine environment, is necessary to support local energy policy and marine planning decisions in a globally changing climate. Moreover, such knowledge could further highlight the mitigation benefits of coastal ecosystems and boost their policy recognition (Hooper et al., 2017; Causon and Gill, 2018; Bindoff et al., 2019).

CRediT authorship contribution statement

H.E.E. Voet: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Resources, Data curation, Writing – original draft, Writing – review & editing, Visualization. **C. Van Colen:** Conceptualization, Methodology, Validation, Resources, Writing – review & editing, Supervision, Funding acquisition. **J. Vanaverbeke:** Conceptualization, Methodology, Validation, Resources, Writing – review & editing, Supervision, Project administration, Funding acquisition.

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.

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Appendices. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2021.152194>.

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