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Effects of CO_2 enrichment on cockle shell growth interpreted with a Dynamic Energy Budget model

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ABSTRACT

The increase in human induced atmospheric CO_2 level leads to an increase in ocean acidification (OA). Mitigation of this increase by storage of CO_2 in abandoned marine oil and gas reservoirs is seen as an interesting cost effective solution. However, this involves a risk of CO_2 loss causing localised reductions in seawater pH. In this paper we report on the effects of CO_2 enhancement on the growth of the bivalve *Cerastoderma edule* in mesocosms. The experiments show significant reductions in shell length, shell weight and cockle flesh dry weight at increased CO_2 level suggesting both direct (shell erosion) and indirect (metabolic) effects. Indirect effects were analysed and interpreted using a Dynamic Energy Budget model by describing changes in 3 metabolic processes: assimilation, maintenance, and growth. Based on cockle size data only we could not differentiate between these processes, however, by using variability of DEB parameter values in 11 bivalve species, we showed growth to be the least relevant process.

1. Introduction

Human fossil fuel combustion is considered a major threat to the marine environment because of atmospheric CO_2 dissolving in seawater and forming carbonic acid (H_2CO_3), which dissociates to bicarbonate (HCO_3^-), carbonate ions (CO_3^{2-}) and protons (H^+) (Cigliano et al., 2010). As a result it contributes to acidification of oceans (OA) which is expected to increase unless CO_2 emissions are dramatically reduced (Doney et al., 2009). Oceans have become more acidic since preindustrial times as is illustrated by the decrease in pH of marine surface waters by 0.1 point (Orr et al., 2005).

Among options to reduce CO_2 emissions, such as the use of less carbon-intensive fuels (nuclear power and renewable energy sources), and enhancement of biological sinks, Carbon Dioxide Capture and Storage (CCS) is seen as feasible and cost effective (ICPP, 2005). A potentially suitable way for CCS is geological storage in abandoned oil and gas reservoirs (Steeneveldt et al., 2006). Injection of CO_2 in reservoirs to enhance the production of oil and gas is already common practice (Tait et al., in press). Storage in sub-seabed oil and gas fields may, however, involve risks of CO_2 leakage. If, as a consequence of e.g. transport pipeline failure, CO_2 is lost into the marine environment considerable localised reductions in seawater pH can be expected to occur (Blackford et al., 2009). Such pH reductions are especially detrimental to species that form calcareous tissues, like molluscs and corals (Hendriks et al., 2010; Hoegh-Guldberg et al., 2007; Kroeker et al., 2010). Many studies report the effects of OA on calcifying organism at various levels of physiological detail (e.g. respiration (Melatunan et al., 2011), neutral red retention (Beesley et al., 2008)). Few, however, are able to interpret the ecological consequences of reported effects, given a lack of an interpretation framework to assess the overall impact. The Dynamic Energy Budget (DEB) theory (Kooijman, 2010; Kooijman and Metz, 1983), provides a logical and consistent framework to integrate the effects of stress factors such as those coming from OA on the vital rates of a species (growth, development, reproduction and survival). Changes in these vital rates directly affect ecologically relevant parameters such as population viability (e.g. Jager and Klok, 2010; Klok and De Roos, 1996). In DEB the impact of OA can be interpreted as a change in the energy flow within an organism. DEB gives mechanistic insight by describing how a change in growth changes reproduction by treating both vital rates as interdependent (Klok, 2007; Kooijman and Metz, 1983). Currently the only application of DEB in describing impacts of OA is on coccolithophores (Muller and Nisbet, in press).

To illustrate possible ecological risks of CCS on vulnerable species we describe in this paper the effects of CO_2 increase on the marine bivalve *Cerastoderma edule* using an existing DEB model.

2. Methods

2.1. Introduction to DEB

DEB theory describes the energy pathways in individuals (Fig. 1). According to DEB theory, a reduction in growth can be caused by reduced assimilation (process of feeding and digestion) (1 in Fig. 1), enhanced

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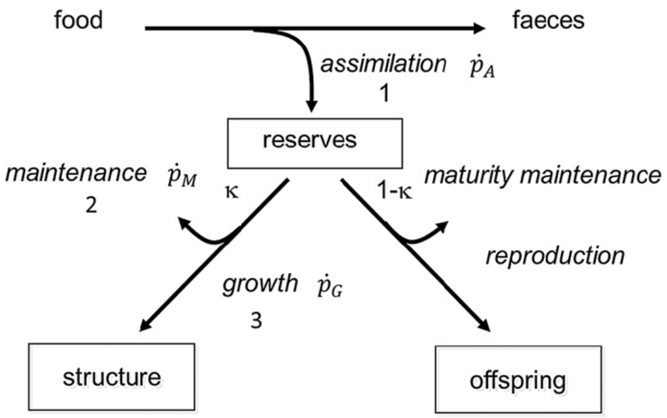

Fig. 1. Schematic representation of the Dynamic Energy Budget model after Kooijman, 2010. When food is assimilated, energy is first transported to a reserves compartment. These reserves introduce metabolic memory and can explain many biological phenomena such as reproduction taking place during starvation. From the reserves, energy is allocated in a fixed ratio (κ) to maintenance and growth of structural elements and investment in reproduction ($1-\kappa$). Maintenance of structural elements always takes precedence over growth, likewise for maturity maintenance. Numbers indicate where growth may be influenced by enhanced CO_2.

maintenance costs (2 in Fig. 1), or enhanced growth costs (3 in Fig. 1). Such changes in the assimilation flux $\dot{p}_A$, the somatic maintenance flux $\dot{p}_M$ and the growth flux $\dot{p}_G$ result from changed underlying DEB parameters. Underlying DEB parameters of interest (see Table 1 for units and description) are the maximum specific searching rate $\{\dot{F}_m\}$ and maximum surface specific feeding rate $\{\dot{p}_{Xm}\}$ for effects on assimilation, the volume specific costs for somatic maintenance $[\dot{p}_M]$ for effects on maintenance, and the volume specific cost of growth $[E_G]$ for effects on growth (Jager et al., 2010; Kooijman, 2010; Muller et al., 2010). For an in-depth derivation and discussion on how DEB parameters relate to the fluxes see Kooijman (2010).

2.2. Description of experiments

2.2.1. Mesocosms

Six outdoor mesocosms were used for this study. Each mesocosm consisted of a glass-fibre tank, partly buried in the ground, with a volume of approximately 5 m^3 (diameter 190 cm, depth 180 cm). All mesocosms were provided with a bottom layer of 20 cm natural sandy sediment, collected from the coastal Dutch North Sea and a 150 cm deep layer of natural seawater collected from the Oosterschelde. The Oosterschelde, a relatively pristine tidal bay in direct connection with the North Sea, is often used as a reference site in marine ecotoxicological studies in the Netherlands (e.g. Foekema et al., 2008, 2012; Kuiper et al., 2007). To attain similar initial conditions, mesocosms were connected by pipes, and seawater was actively circulated by a pump for 39 days. Mesocosms were disconnected one day before the start of the exposure experiment. Sufficient mixing of the water column during the exposure experiment was ensured by continuous aeration at about 10 cm above the sediment in the centre of each mesocosms. On top of the mesocosms transparent lids were placed to shelter against rainfall. Evaporation losses were replenished with demineralised water so that salinity was maintained throughout the study at 31 ± 1‰.

Table 1
Units and description of parameters used. Parameters expressed per unit of structural volume have square brackets [] and quantities per unit of structural surface area have braces {}.

Parameter	Unit	Description
AE	–	Absorption efficiency assimilated Food
$[E_G]$	J cm^{-3}	Volume specific costs of structural growth
f	–	Scaled functional response: $f = \frac{X}{(X_K + X)}$
$\{\dot{F}_m\}$	J $cm^{-2} \cdot d^{-1}$	Maximum surface specific searching rate
κ	–	Allocation fraction to soma
L	cm	Volumetric structural length
L_m	cm	Maximum volumetric structural length
$\{\dot{p}_{Am}\}$	J $cm^{-2} \cdot d^{-1}$	Maximum surface specific feeding rate
$[\dot{p}_M]$	J $cm^{-3} \cdot d^{-1}$	Volume-specific somatic maintenance rate
$\{\dot{p}_{Xm}\}$	J $cm^{-2} \cdot d^{-1}$	Maximum surface specific feeding rate
X	μg Chl-a $\cdot l^{-1}$	Food concentration
X_K	μg Chl-a $\cdot l^{-1}$	Half saturation constant
z	–	Zoom factor: $L_m/L_m^{ref}, L_m^{ref} = 1cm$

Phyto- and zooplankton and small benthic invertebrate species were already introduced with water and sediment. Macro invertebrates, representatives from various taxonomic classes that are commonly present in shallow soft sediment coastal ecosystems, were introduced the first week after establishment of the mesocosms to mimic natural conditions. In each mesocosm 50 common periwinkles (*Littorina littorea*, gastropod), 2 pieces of breadcrumb sponge (*Halichondria panacea*, sponge) and approximately 100 mudshrimps (*Corophium volutator*, amphipod) were allotted randomly. All introduced fauna was collected at relatively pristine field locations in the Dutch Wadden Sea.

2.2.2. Test organism and test condition

Common cockles (*Cerastoderma edule*, bivalve), collected in early May 2012 at tidal flats of the Dutch Wadden Sea near the town of Den Helder, were randomised in seven groups of 25 individuals each (shell length 18.0 ± 0.6 mm, wet weight 1.74 ± 0.2 g). One group was frozen and stored for later measurements of initial conditions (e.g. flesh weight). The remaining six groups were transferred to the six mesocosms (two duplicated treatments and two controls). Of each cockle the shell length (longest possible) and wet weight were measured before being placed on the sediment in an individual enclosure, such that each individuals growth pattern could be monitored.

Mesocosms were continuously aerated with 1300 ml min^{-1} compressed air from the centre, just above the sediment surface. Four mesocosms were provided additionally with 75 ml min^{-1} CO_2 (Foodgrade, supplier Linde Gas BV, Netherlands) from the same point over a period of 55 days starting from the 8th of May 2012. This CO_2 flux was based on (Blackford et al., 2009) who estimated a drop in pH of 1 to 2 units as worst case risk for sub-seabed CO_2 storage as a consequence of transport pipeline rupture, and earlier studies using the same mesocosms in which a CO_2 flux of 75 ml min^{-1} caused such a drop in pH (unpublished data). In two of the four mesocosms this CO_2 flux was continuous. Because exposure to benthic organisms is variable as a result of tidal currents (Blackford et al., 2009), the CO_2 flux was interrupted every 6 h in the other two mesocosms to mimic tidal changes.

2.2.3. Sampling and analyses

In the first days of the exposure experiment the pH was measured three times a day in order to determine daily pH fluctuations in the tidal mesocosms. These fluctuations did not exceed 0.2 pH units and were not considered relevant. Therefore, during the rest of the exposure experiment the pH was determined with the same frequency (twice a week) as dissolved oxygen concentration, salinity and water temperature, by submerging electrodes (PHC101, Hach LDO101, and CDC401) half way in the water column. Water samples were collected twice a month for the analyses of HCO_3, Dissolved Organic Carbon (DOC), inorganic nitrogen, ortho-phosphate, and silicate (see Table A1). Phytoplankton biomass was measured in water samples as chlorophyll-a (Chl-a) concentration twice a week by means of a 1 Hz-kuvetten Fluorimeter (BBE-Moldaenke; Celussi and Cataletto, 2007).

Over the test period oxygen was fully saturated (over 90%), and the pH equalled 8.3 ± 0.1, 6.95 ± 0.2 and 6.7 ± 0.2 in the control, for continuous and tidal mesocosms, respectively. Temperature (average 16.9 ± 2.7 °C) and Chl-a increased over time, and the last varied between treatments (Fig. 2).

The cockles were weighed (total wet weight after drying the shell with a paper tissue) and their shell length was measured using a pair of digital callipers, at the start of the experiment, at day 27 and at day