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Tolerance of allogromiid Foraminifera to severely elevated carbon dioxide concentrations: Implications to future ecosystem functioning and paleoceanographic interpretations

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ABSTRACT

Increases in the partial pressure of carbon dioxide (pCO_2) in the atmosphere will significantly affect a wide variety of terrestrial fauna and flora. Because of tight atmospheric–oceanic coupling, shallow-water marine species are also expected to be affected by increases in atmospheric carbon dioxide concentrations. One proposed way to slow increases in atmospheric pCO_2 is to sequester CO_2 in the deep sea. Thus, over the next few centuries marine species will be exposed to changing seawater chemistry caused by ocean–atmospheric exchange and/or deep-ocean sequestration. This initial case study on one allogromiid foraminiferal species (*Allogromia laticollaris*) was conducted to begin to ascertain the effect of elevated pCO_2 on benthic Foraminifera, which are a major meiofaunal constituent of shallow- and deep-water marine communities. Cultures of this thecate foraminiferan protist were used for 10–14-day experiments. Experimental treatments were executed in an incubator that controlled CO_2 (15 000; 30 000; 60 000; 90 000; 200 000 ppm), temperature and humidity; atmospheric controls (i.e., ~375 ppm CO_2) were executed simultaneously. Although the experimental elevated pCO_2 values are far above foreseeable surface water pCO_2, they were selected to represent the spectrum of conditions expected for the benthos if deep-sea CO_2 sequestration becomes a reality. Survival was assessed in two independent ways: pseudopodial presence/absence and measurement of adenosine triphosphate (ATP), which is an indicator of cellular energy. Substantial proportions of *A. laticollaris* populations survived 200 000 ppm CO_2 although the mean of the median [ATP] of survivors was statistically lower for this treatment than for that of atmospheric control specimens. After individuals that had been incubated in 200 000 ppm CO_2 for 12 days were transferred to atmospheric conditions for ~24 h, the [ATP] of live specimens (survivors) approximated those of the comparable atmospheric control treatment. Incubation in 200 000 ppm CO_2 also resulted in reproduction by some individuals. Results suggest that certain Foraminifera are able to tolerate deep-sea CO_2 sequestration and perhaps thrive as a result of elevated pCO_2 that is predicted for the next few centuries, in a high-pCO_2 world. Thus, allogromiid foraminiferal "blooms" may result from climate change. Furthermore, because allogromiids consume a variety of prey, it is likely that they will be major players in ecosystem dynamics of future coastal sedimentary environments.

1. Introduction

The partial pressure of carbon dioxide (pCO_2) in the atmosphere has oscillated between 177 and 300 ppm over the past ~800 000 years (Lüthi et al., 2008), until the Industrial Revolution in the mid-1800s. Since then, atmospheric pCO_2 has increased to today's concentration of ~375 ppm. The atmospheric pCO_2 has increased dramatically in the past several hundred years due to both anthropogenic causes and natural processes (e.g., Sabine et al., 2004). Because CO_2 is a greenhouse gas that contributes to global warming, society would benefit from the identification of effective means to minimize the increase of atmospheric pCO_2. Several methods of CO_2 sequestration have been proposed, including geological sequestration in aquifers or subsurface deposits, terrestrial biological sequestration via copious planting of trees, and oceanic sequestration via iron seeding or deep-ocean injection (reviewed in Yamasaki, 2003). Deep-ocean injection of CO_2 extracted from gases released by industrial activities could potentially slow and minimize global warming by removing CO_2 from emission sources and pumping it as a gel-like liquid into mid-

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ocean depths or sea-floor depressions where it could dissipate over millennial time scales (e.g., Haugan and Drange, 1992; Brewer et al., 1998, 2005).

Because a large percentage of Earth's carbon dioxide is naturally sequestered in the oceans, deep-ocean CO_2 sequestration continues to receive dedicated study as a feasible method to minimize rates of atmospheric pCO_2 rise (e.g., Hove and Haugan, 2005; White et al., 2006; Wannamaker and Adams, 2006; Brewer et al., 2006). Although carbon dioxide is also naturally stored in the oceans, the effect of artificially elevated levels of pCO_2 on the ocean's inhabitants and global ecosystem balance is unclear. An increase in pCO_2 results in decreases in both pH and carbonate ion concentration, each of which has important biological implications. Biochemical factors to contemplate when considering exposure to high pCO_2, or hypercapnia, are acid-base imbalances, the potential toxicity of CO_2 on respiration via disruption of oxygen-transport mechanisms, and metabolic suppression that retards growth and reproduction (e.g., Seibel and Walsh, 2001; Pörtner et al., 2004). Acid-base imbalances are especially important for taxa with calcareous exoskeletons because the more acidic conditions in the ocean's water column will lead to shell dissolution. Sub-lethal effects of elevated pCO_2 in animals include reduced activity and loss of consciousness; if impeded oxygen transport persists, death may result (Seibel and Walsh, 2001). Thus, while the deep sea may provide an appealing destination for CO_2 disposal to mitigate global warming, the negative effects of the elevated pCO_2 may outweigh the advantages (e.g., Tyler, 2003; Pörtner et al., 2005). By understanding the effects of deep-sea CO_2 sequestration on all major taxa, we can better predict future ecosystem functioning to enable better-informed policy decisions.

The effect of carbon dioxide disposal on deep-sea organisms has received much study over the last few years but is still poorly understood. It has been established that fish and other megafauna, even though mobile, do not necessarily escape enhanced pCO_2 (Tamburri et al., 2000); severe physiological effects can be long lasting or lethal (e.g., Seibel and Walsh, 2003). There is limited knowledge of the effects of deep-ocean CO_2 sequestration on microbial communities, although it has been shown that CO_2 sequestration inhibits marine nitrification (Huesemann et al., 2002). Information on the metazoan meiofaunal community response to deep-sea CO_2 disposal suggests that copepod biodiversity is negatively affected (e.g., Kurihara et al., 2004; Thistle et al., 2005), harpacticoid copepods attempt to escape CO_2-rich seawater (Thistle et al., 2007), and nematode abundance and specimen size decrease (Fleeger et al., 2006). Other studies assessing the effects of CO_2 sequestration on deep-sea meiofauna agree that metazoan abundances decrease (Barry et al., 2004; Ishida et al., 2005) but, interestingly, bacterial respiration rates increase (Ishida et al., 2005). Thus, the effect of CO_2 sequestration on the deep-sea benthos is a complex relationship (Ishida et al., 2005).

This study investigates the effects of elevated CO_2 on a ubiquitous protistan constituent of marine microbial systems: allogromiid benthic Foraminifera. The response of marine protists to pCO_2 sequestration has only been recently documented via field studies (e.g., Barry et al., 2005; Ricketts et al., in revision). In this laboratory study, Foraminifera were targeted for a number of reasons. First, they are an important link in the marine food web (e.g., Legendre and Le Févre, 1995; van Oevelen et al., 2006; Rowe et al., 2008). Second, they can be the dominant meiofaunal taxon in deep-sea sediments (e.g., Coull et al., 1977; Snider et al., 1984; Gooday et al., 2000). Third, because of their relatively slow migration rates (e.g., Gross, 2000), elevated pCO_2 may be more deleterious to them compared to mobile metazoans. Fourth, certain Foraminifera are easily cultured in the laboratory, and thus, provide plentiful populations for experimentation (e.g., Lee and Pierce, 1963; Hintz et al., 2004). Of the three types of Foraminifera (i.e., calcareous, agglutinated, thecate), this initial case study used a thecate shallow-water species to allow experimentation at room temperature and atmospheric pressure.

2. Materials and methods

Allogromia laticollaris cultures, which were obtained originally in 2004 from J. Travis, were grown in a mixture of 32‰ seawater and Alga-Gro® seawater medium (Carolina Biological Supply) in 20 mL glass tubes with loose caps (modified from Travis and Allen, 1981). Each week, each culture tube received ~2 mL of concentrated algae comprised of an equal proportion of both *Dunaliella tertiolecta* and *Isocrysis galbana* to serve as foraminiferal food. Cultures were maintained at ~23 °C and in a 12 h light-dark cycle.

For each experiment, the full size spectrum of ~100 *A. laticollaris* was removed from a culture tube via pipette; ~25–30 individuals and minimal residual algal material were placed in each of three 3.5-cm diameter Petri dishes containing 32‰ artificial seawater. Two of these dishes were placed in a Nuaire US Autoflow CO_2 Water-Jacketed incubator (NU4950) that was attached to a Thermo RTE740 refrigerated bath to maintain temperature at 22–23 °C for the duration of the experiment (i.e., 10–14 days). The darkened incubator was maintained at 75–85% humidity during each experiment. One of these Petri dishes was denoted the experimental (CO_2) treatment and the other as the Rebound (see below). The third of these dishes was placed in a humid chamber, which was housed in a darkened cabinet for the duration of the experiment; for these dishes, the temperature ranged from 21–

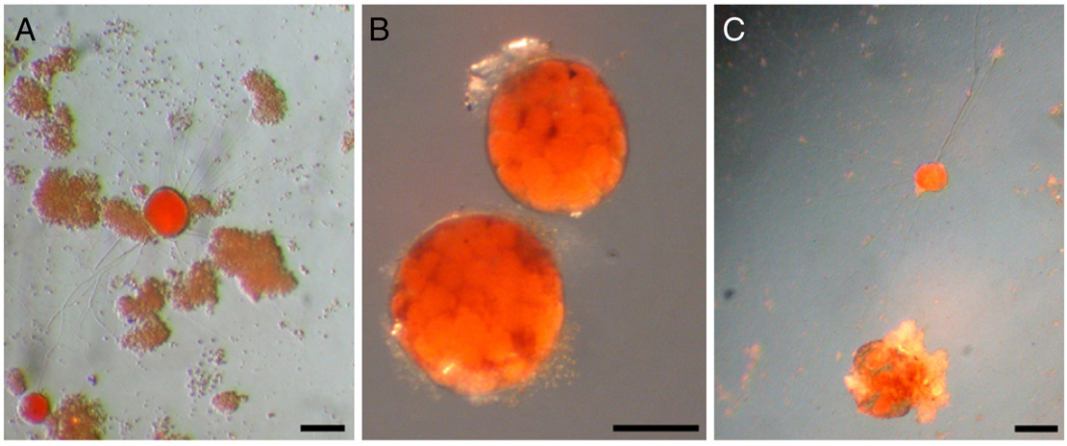

Fig. 1. Transmitted light micrographs of *Allogromia laticollaris*. A. Rebound specimen after exposure to 200 000 ppm CO_2 for 12 days, with extended pseudopodial network. B. Specimens, exposed to 90 000 ppm CO_2 for 14 days, encasing dozens of offspring. C. Individual (lower center) that reproduced during exposure to 90 000 ppm CO_2 for 14 days, four days after return to atmospheric conditions. Note that many offspring, one of which is visible with extended pseudopods, have dispersed; approximately 6 remain in the parental test. Scale bars: A = 100 µm; B, C = 50 µm.