

Simulated sequestration of industrial carbon dioxide at a deep-sea site: Effects on species of harpacticoid copepods

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Abstract

One proposal for alleviating global warming is to sequester large amounts of industrial carbon dioxide on the deep-sea floor, but the environmental consequences of sequestration for the animals living in the sediment are poorly known. In an earlier publication, we reported that, during an experimental sequestration off central California (36.378°N, 122.676°W, 3262 m depth), most individuals of our target taxon (the harpacticoid copepods) were killed, but ~20% survived. Because knowledge of which species survived and how they did so could clarify the effects of sequestration on the fauna, we have now identified the individuals from that experiment to species. Although most were adversely affected, species differed significantly in the degree of their susceptibility. Unexpectedly, six species showed no effect and may be resistant. The hypothesis that harpacticoids could escape the effects of carbon dioxide-rich seawater by moving deeper into the seabed was not supported. Exposure to carbon dioxide-rich seawater created partially defaunated areas, but we found no evidence that disturbance-exploiting harpacticoid species invaded during the recovery of the affected area. Because the environmental effects of the carbon dioxide (e.g. unusually acidic pore water) were still present, however, the opportunity for invasion might not yet have occurred. Differences among species in susceptibility increase the complexity of the effects of carbon dioxide sequestration on the deep-sea fauna.

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1. Introduction

Since the beginning of the industrial revolution, the concentration of carbon dioxide in the atmosphere has increased from 275 to 370 parts per million (Hoffert et al., 2002), largely as a consequence of the burning of fossil fuel (Keeling and Whorf, 1998). Because carbon dioxide interferes with the transmission of infrared

radiation from Earth into space, the increase is thought to be causing the atmosphere to warm. Carbon dioxide is transferred naturally from the atmosphere to the ocean, but the rate is low relative to the rate at which humans produce it, so the atmospheric concentration continues to rise (Reichle et al., 1999). Realistic assessments of future fossil-fuel burning (Joos et al., 1999; Marland et al., 2001) indicate that this imbalance will continue, the planet will warm, climatic bands will shift poleward, and sea level will rise.

Because most fossil-fuel carbon dioxide that enters the atmosphere will eventually be transferred to the

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ocean, one proposal is to collect it at point sources, such as power plants, and to inject it directly into the ocean, where it would stay for hundreds of years (Marchetti, 1977; Ormerod et al., 2002). Sequestration of carbon dioxide in the ocean by direct injection in amounts that would contribute meaningfully to decreasing the rate of global warming appears to be possible (IPCC (Intergovernmental Panel on Climate Control), 2001), but before policy makers adopt such an approach, the environmental consequences must be known.

Carbon dioxide can directly affect the physiology of organisms, for example, by causing respiratory distress (Tamburri et al., 2000). It can also affect organisms indirectly. For example, an increase in its concentration decreases the pH of seawater, producing a variety of physiological consequences (Pörtner et al., 2004). Relatively little is known about the effects of elevated carbon dioxide concentration on deep-sea animals. Ordinarily, they experience an environment of great physicochemical constancy and are thought to be poorly adapted to dealing with environmental changes (Shirayama, 1995, 1997; Seibel and Walsh, 2001, 2003), but research has just begun (Tamburri et al., 2000; Barry et al., 2004, 2005).

We have previously reported on an experiment in which we placed ~20 L of liquid carbon dioxide on the seafloor in each of three open-topped containers at 3262 m depth. After 29 days, the pH of the pore water in the upper 8 mm of the sediment ~40 m away from the containers was as expected for this region (Barry et al., 2004), but that ~2 m away from the nearest container was ~0.8 unit more acidic. We first reported that, contrary to expectation, the abundance of harpacticoid copepods (and other meiofauna) near the containers did not differ from that far from the containers (Carman et al., 2004), but we later ascertained that significantly more of the harpacticoids in cores taken near the containers than of those in cores taken farther away were dead at the time of collection (Thistle et al., 2005). We concluded that the numbers we reported from areas near the containers were overestimates because they included harpacticoids killed by carbon dioxide-rich water that had not decayed away before they were collected (Carman et al., 2004; Thistle et al., 2005), which is plausible given the slow growth of free-living microbes in the deep sea (Jannasch et al., 1971).

A striking feature of our later results (Thistle et al., 2005) was that ~20% of the harpacticoid individuals that had been exposed to carbon dioxide-rich seawater were alive when collected. Because knowledge of which species survived and how they did so could clarify the effects on the infauna of sequestered carbon dioxide, we

investigated the distribution of susceptibility among species. We formulated and tested two hypotheses: first, that harpacticoids could escape the effects of carbon dioxide-rich seawater by burrowing deeper into the sediment and, second, that some or all of the individuals that were alive when collected were members of disturbance-exploiting species that had arrived after the effects of the carbon dioxide-rich seawater had moderated. To test the first, we compared, for each species thought to be alive when collected, the depth of its occurrence near the containers with that far from the containers. To test the second, we asked whether individuals thought to be alive when collected were from species that were rare in the background community, as is common for disturbance-exploiting species (Grassle and Morse-Porteous, 1987; Snelgrove et al., 1994). Finally, to determine whether Carman et al.'s (2004) conclusions about the environmental impact of carbon dioxide sequestration, which were based on abundance, would have been different if they had been based on species composition, we compared the species composition of the area near the containers to that far from them.

2. Materials and methods

2.1. Study site, experimental setup, and sampling

At the study site (Barry et al., 2005, Experimental CO₂-4) off central California in the axis of Monterey Canyon (36.378°N, 122.676°W, 3262 m; Fig. 1), the sediment was a fine mud to a depth of many centimeters. At the time of our work, bottom-water temperature was 1.6 °C, the oxygen concentration was 60.0 to 60.5 μM, and salinity was 34.6. Mean current speed, measured 8 m above the bottom with an acoustic-Doppler current meter (RDI Sentinel) was 5.7 cm s⁻¹. Currents were aligned with the axis of the canyon; net flow was 2.3 cm s⁻¹ in the up-canyon direction.

All manipulations on the sea floor were performed with the remotely operated vehicle *Tiburion* operated by the Monterey Bay Aquarium Research Institute. Barry et al. (2005) gives details of the experimental design. Briefly, we created open-topped containers for carbon dioxide on the seafloor by setting sections of plastic pipe (48 cm internal diameter by ~15 cm long) on their sides in the sediment such that ~15 cm extended above the seabed (Carman et al., 2004, their Fig. 2). One container was placed at each apex of an imaginary equilateral triangle ~4 m on a side (Fig. 2). Each container was filled with ~20 L of carbon dioxide, which is liquid and denser than seawater at this depth.

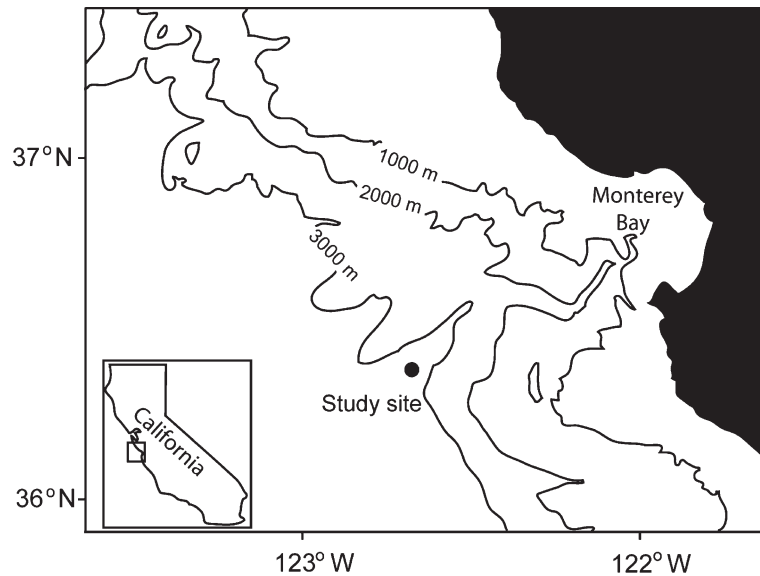


Fig. 1. Chart of the eastern North Pacific off central California showing the location of the study site.

As reported in Carman et al. (2004), we returned to the site after 29 days and collected cores (7-cm inner diameter) ~2 m away from one of the containers (=Near cores) and ~40 m from the containers (=Far cores), where the effects of carbon dioxide were expected to be minimal or nonexistent (Barry et al., 2004; Fig. 2). Within both Near and Far areas, the cores were separated from each other by ~20 cm. After the *Tiburón* returned to the surface, the cores were placed temporarily in a 4 °C cold room. We processed a Far core first and then alternated Near and Far cores.

Because carbon dioxide concentration is difficult to measure at the spatial resolution we required, we used pH as a surrogate, as is commonly done (Tamburri et al., 2000; Barry et al., 2003, 2004). We measured pH

profiles in the cold room using an externally calibrated Unisense® pH microelectrode (tip diameter=100 µm) that was mounted in a micromanipulator and connected to a Knick® Portamess 913 pH meter. For each core, we measured pH at 250-µm intervals from 2 mm above the sediment surface to 8 mm below.

After measuring pH, we removed the seawater from the core, pushed the sediment to the top of the tube, and inserted a 1.9-cm (inner diameter) subcorer in the center. We then extruded the sediment and removed the portion surrounding the subcore in four depth intervals: 0–5, 5–10, 10–20, and 20–30 mm. (The material in the subcore was not used in this study.) The seawater mentioned above was sieved on a 32-µm-aperture sieve, and the sieve contents were added to the 0- to 5-mm layer sample. Each layer was preserved in a solution of formaldehyde and 35 ppt artificial seawater (1:9 v/v) and buffered with sodium borate. In the laboratory, the material was stained with rose bengal for easier and more accurate sorting.

2.2. Study organisms

We were interested in effects on submillimeter-sized metazoans, a size class that includes nematodes, harpacticoid copepods, ostracods, the immature stages of many macrofaunal species, etc. All such animals could not be studied because they were very numerous, but because susceptibility to stress scales with size, we felt that a study of a representative taxon would be revealing. We focused on the harpacticoid copepods

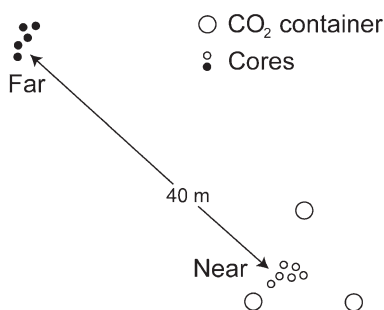


Fig. 2. A representation of the study site (not to scale) showing the arrangement of the containers of carbon dioxide and the cores. Cores labeled Near were taken ~2 m from the nearest container; those labeled Far were taken ~40 m from the containers. Containers were separated by ~4 m (Barry et al., 2005).

because they occur throughout the deep sea in large numbers. These miniature crustaceans were removed from the sieved material under a dissecting microscope. Under a compound microscope, adults were identified to sex and working species and stored in glycerin drops on glass slides. Juveniles could not be identified reliably because many species only develop their distinguishing features as adults. Because few deep-sea harpacticoid species have been described, we created a key to our working species and identified them to the lowest possible taxon using Wells (1977), Huys et al. (1996), and the primary literature.

2.3. Degree of decay

Individuals of species more susceptible to carbon dioxide-rich seawater should have died earlier in the experiment and have decayed more than individuals of more-resistant species by the time of sampling. We therefore inferred each individual's susceptibility to carbon dioxide exposure from the extent of its decay, an inference supported by data given in Thistle et al. (2005). One of us, who did not know its provenance, assigned each individual to one of five stages of decay (Table 1). Note that more-decayed animals were assigned larger numbers.

2.4. Differences in susceptibility among species

We determined the stage of decay of each individual of each species in the combined 0- to 5- and 5- to 10-mm layers of each core, because individuals in them were most likely to have been exposed to the carbon dioxide-rich seawater. From the decay scores, we calculated the average stage of decay for each species in each core. For each species, we calculated two-tailed, 95% confidence limits of the difference in these averages between Far cores and Near cores using randomization (Simon, 1999). Species that were not present in both Far and Near cores or that occurred in only one core in each data set were omitted.

Table 1
Descriptions of the states of individuals assigned to each stage of decay

Description	Stage of decay
Internal organs fill exoskeleton; muscles well defined	1
Urosome or prosome muscles partially gone	2
Urosome and prosome muscles mostly gone, but some muscle remaining in cephalosome	3
Only gut lining remaining	4
Exoskeleton empty	5

2.5. The average depth of a species

To obtain a depth score for each species in each core, we assigned each individual to the center of the layer in which it was found; e.g., individuals in the 0- to 5-mm layer were considered to be at 2.5 mm depth. We calculated the average depth in the top 3 cm of the sediment for each species in the Far and in the Near cores separately. For each species whose average depth in the Near cores exceeded that in the Far cores, we tested for a significant difference using randomization (Simon, 1999), except when the species occurred in so few cores that detection of a significant difference was mathematically impossible.

2.6. Detecting disturbance-exploiting species

To determine whether individuals that appeared to be alive when we sampled belonged to species that were rare in or absent from the background community (i.e., disturbance-exploiting invaders), we selected species whose average stage of decay was less than or equal to 2 in the top two layers of Near cores. We used randomization (Simon, 1999) to determine whether the average abundance of these species was greater in Near than in Far cores.

2.7. Comparison of species composition

To compare the species compositions of Near and Far cores, we used the abundance data for each species from the top two layers of each core. We square-root transformed the data to reduce the influence of abundant species and calculated Bray–Curtis similarities between all possible pairs of cores. We used nonparametric analysis of similarity (the ANOSIM module of the PRIMER® 5.2.8 software package, Clarke and Gorley, 2001) to determine whether the fauna of the Near cores differed from that of the Far cores.

Given the exploratory nature of this study, we made no adjustment for multiple testing in any analysis.

3. Results

3.1. pH

When we injected the carbon dioxide, it was visible in the containers, but when we returned 29 days later, none could be seen in the containers or on the seafloor. We inferred that it had dissolved into the overlying seawater and that the carbon dioxide-rich seawater, which is slightly denser than ordinary seawater, flowed

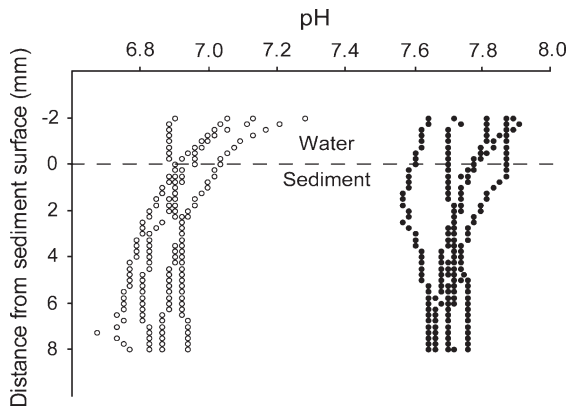


Fig. 3. Profiles of pore-water pH showing that it was substantially lower ~2 m from the nearest container of carbon dioxide (O) than ~40 m away (●).

over the sediment near the containers. An in situ pH profile measured during a subsequent experiment was consistent with this view.

The pH profiles (Fig. 3) in some cores in the present experiment were more or less vertical, indicating that some mixing had occurred during sampling or recovery. The inadvertent mixing did not mask the striking difference in pH of the pore water between the Near and Far cores. The Far cores clustered around pH 7.7, a reasonable value for this region and depth (Barry et al., 2004). The Near cores clustered around pH 6.9. The measurements for the Near and Far cores did not overlap.

3.2. Distribution of susceptibility among species

As is typical for deep-sea harpacticoids (Thistle, 1978), a large number of species (67) were present at the study site in the 0- to 3-cm layer, and many were rare. We calculated 95% confidence limits on the difference in average stage of decay between Far and Near cores for 34 testable species from the combined 0- to 5- and 5- to 10-mm-layer data (Fig. 4). Eighteen species were significantly more decayed in the Near than in the Far cores. Unexpectedly, one species was significantly less decayed. The confidence intervals of many pairs of species did not overlap, so many species differed in susceptibility to carbon dioxide-rich seawater.

3.3. Species' depth differences between Near and Far cores

Of the 42 species that were present in both Near and Far cores, weighted average depth was greater in Near than in Far cores for 10 species. Five of these species occurred in enough cores to allow a test in which a significant difference could have been detected, but none occurred significantly deeper in Near than in Far cores.

3.4. Detecting disturbance-exploiting species

The combined data from the 0- to 5- and 5- to 10-mm layers contained 19 species that appeared to be alive at

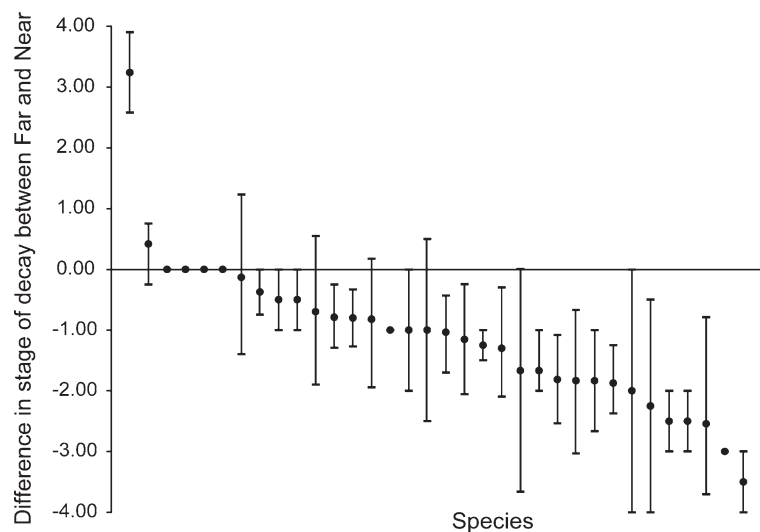


Fig. 4. The difference in average stage of decay between Far and Near cores by species, showing that species differed in susceptibility. Note that a positive number indicates that a species was less decayed in Near than in Far samples. Error bars are two-tailed, 95% confidence limits. For some species, all individuals were in the same state of decay, so the confidence limits were zero.

the time of collection in the Near cores. Of these, 10 were more *abundant* in the Near cores than in the Far cores, but only 4 occurred in enough cores that a significant difference could have been detected. For none of these species was the average abundance in Near cores significantly different from that in Far cores.

3.5. Comparison of species composition

The two-tailed probability that the faunas of the Near and Far cores would be as different or more different by chance was 0.615, which was not significant.

4. Discussion

4.1. pH

Our pH profiles showed that the pore water of the Far cores had pH values comparable to those reported for this region and depth in the North Pacific (Barry et al., 2004) but that the pore water in the Near cores was significantly lower. We therefore concluded that we had successfully created an experimental difference in exposure to carbon dioxide-rich seawater.

4.2. Distribution of susceptibility among species

Setting aside regions such as hydrothermal vents, cold seeps, and oxygen-minimum zones, the chemistry of seawater in the deep sea varies little at the time and space scales that individual deep-sea animals experience (Gage and Tyler, 1991). Deep-sea animals have therefore been expected, notably by Shirayama (1995, 1997) and by Seibel and Walsh (2001, 2003), to be unusually sensitive to variation in their chemical environment, in particular, to the changes that would be caused by carbon dioxide sequestration. This expectation has been confirmed for nematodes, euglenoid flagellates, amoebae (Barry et al., 2004, 2005), and harpacticoid copepods taken as a group (Thistle et al., 2005). In our study, the vast majority of species were on average more decayed (i.e., more individuals were dead at the time of sampling) in cores exposed to carbon dioxide-rich seawater than in cores that had experienced only ambient seawater (Fig. 4), extending the support for Shirayama's and Seibel and Walsh's inference to the species level.

When we compared the susceptibilities of different species, we found many significant interspecific differences. These differences could affect the pattern of recovery from carbon-dioxide exposure of the harpacticoid fauna of an area where mortality is not total because more resistant species can be expected to have

advantages during recovery. For example, adults of species already in place could interfere with the settlement of larvae of recolonizing species (see Woodin, 1976). These founder effects could persist for generations and would delay the return of the community to its original state.

We found six species that appeared to be less decayed or no more decayed in Near than in Far cores (Fig. 4). The results for these species could arise if individuals from areas not affected by carbon dioxide-rich seawater moved into the affected areas, arriving just before we sampled. We have also observed that the movement of fishes resuspends surface sediment from time to time and could inject harpacticoids into the water, where currents could have brought them near the containers. Alternatively, these species might be unaffected by the almost order-of-magnitude change in pH to which our experiment exposed them, contrary to Shirayama's (1995, 1997) and Seibel and Walsh's (2001, 2003) expectations (see also Tamburri et al., 2000). Existence of unaffected species would accentuate the potential effects on recovery.

Vopel et al.'s (1998) work suggests a possible explanation for differences in susceptibility. In shallow-water harpacticoid species, individuals with large energy reserves survived physiological stress better than individuals with small reserves. If deep-sea species depend on energy reserves to withstand the physiological stresses caused by exposure to carbon dioxide-rich seawater and differ in the amount of energy they routinely store, they would vary in susceptibility, as we observed. Similarly, the differences in susceptibility that we found among individuals within species (data not shown) could arise from differences in their recent history of energy acquisition and expenditure.

4.3. Did species find a refuge at depth in the sediment?

Our pH measurements did not extend deep enough for us to determine the depth of penetration of the pH anomaly and thus whether a refuge existed for harpacticoid species at depth in the sediment. In a subsequent experiment, pH was normal in the 10- to 20-mm layer, suggesting that the 20- to 30-mm layer in our experiment was also unaffected by carbon dioxide-rich seawater. The species that we found to be susceptible to carbon dioxide exposure can live under the conditions that normally occur in the 20- to 30-mm layer, because we found individuals of these species that were alive at the time of collection in that layer in Far cores. A refuge from the acidic pore water therefore probably existed in the 20- to 30-mm layer, but we found no

evidence that susceptible harpacticoid species used it. Perhaps deep-sea harpacticoids are not accustomed to seeking refuge from a stress at depth in the sediment. Alternatively, because carbon dioxide-rich seawater has a narcotic effect (Tamburri et al., 2000), the initial contact may have stunned the harpacticoids, which remained in place and subsequently died. Whatever the reason, the consequence is clear. The vast majority of adult harpacticoids inhabit the upper layers. For example, of the adults in the 0- to 30-mm layer of our Far cores, an average of 93.2% was in the 0- to 20-mm layer. Therefore, the bulk of the harpacticoid fauna will be exposed to carbon dioxide-rich seawater.

4.4. Were disturbance-exploiting species present?

The portion of our study site exposed to carbon dioxide-rich seawater was disturbed if only because much of the harpacticoid fauna in it was dead (Thistle et al., 2005). It should have been attractive to disturbance-exploiting harpacticoids, but we found no evidence that it was. The results suggest that, to the extent that invasion by such species on this time scale is an ordinary part of patch recovery, it will be disrupted in patches exposed to carbon dioxide-rich seawater.

Disturbance-exploiting harpacticoids might simply have been absent from our area, but we consider this explanation unlikely because one of us (Fleeger, personal observation) has found such a species in another study. We suspect that the continued presence of acidic pore water made the patch unattractive to disturbance-exploiting harpacticoids.

4.5. Carman et al. (2004) reconsidered

Carman et al. (2004) found no difference in harpacticoid abundance between Near and Far cores but suggested that this result would arise if exposure to carbon dioxide-rich seawater had killed the harpacticoids and their corpses were counted along with live individuals. Under this hypothesis, the species composition of the harpacticoid fauna of Near and Far cores should be indistinguishable, as we found it to be, and the animals in Near cores should be more decayed than those in Far cores, as Thistle et al. (2005) found them to be. Together, these results support Carman et al.'s (2004) inference (see also Barry et al., 2004).

4.6. Other comments

Twenty-nine days after the deployment of the carbon dioxide, ~80% of the harpacticoids were dead in an area

~2 m away from the nearest container (Thistle et al., 2005). These dead harpacticoids should have attracted consumers, because necrophagy is common in the deep sea (Thistle, 2003). Because the corpses were still present, this opportunity was not exploited. We speculate that the animals that otherwise would have fed on the corpses either were repelled by the low pH of the pore water (see Tamburri et al., 2000) or were themselves killed by it. For example, protists consume meiofaunal corpses (Tietjen, 1967) but can be killed by carbon dioxide-rich seawater (Barry et al., 2004).

Any method of deep-ocean sequestration will produce a gradient of decreasing carbon dioxide concentration with distance from the injection point. The results of Barry et al. (2003, 2004), Carman et al. (2004), and Thistle et al. (2005) have shown that exposure to carbon dioxide-rich seawater kills small, deep-sea, sediment-dwelling animals, which are very abundant in the deep sea (Thiel, 1979). Therefore, one of the steps in evaluating the merits of deep-ocean sequestration will be to learn where, along the concentration gradient, conditions become benign for these animals (see Barry et al., 2005).

5. Conclusions

As expected, many species of harpacticoids were susceptible to changes in their environment caused by exposure to carbon dioxide-rich seawater, but some species were significantly less susceptible than others. The differences in susceptibility among species did not seem to involve sheltering in sediment layers below those affected by carbon dioxide-rich seawater, so species probably differed in their physiological capacities to withstand the exposure. As a result, recovery of exposed patches may be controlled not only by differences among species in colonization ability but also by their differing tolerances to lingering effects of exposure to carbon dioxide-rich seawater.

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