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Oceanic disposal of CO_2: Potential effects on deep-sea plankton and micronekton—A review

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Abstract: Several general features of the deep-sea ecosystem can be summarized as: (1) the deep sea is a geochemical sink, (2) biomass declines rapidly with depth below 1000 m, and (3) species richness increases to a maximum at about 1000 m depth for pelagic species. Our knowledge of deep-sea plankton and micronekton is, however, still patchy and insufficient. In concern with the feasibility of CO_2 disposal in the deep sea, at present, prior to any categorical decisions being made, more detailed research is needed on the potential effects of lowered pH and raised partial pressure of CO_2 over the entire life of zooplankton and micronekton under realistic hydrostatic pressures. Considering the possibility of CO_2 discharge and of CO_2 retrieval if necessary, confined release of CO_2 in restricted depression of the seafloor at depths greater than 3000 m will be better than dispersion in midwater.

Key words: oceanic CO_2 disposal, deep-sea organism, global waste management, ecology of plankton and micronekton

Introduction

Under the present political, economic and technological disparities of different countries of the world, it seems optimistic to expect to drastically reduce the amount of CO_2 discharged by human activities, e.g. combustion of fossil fuels, deforestation, inefficient technologies in manufacture, etc. within a few decades. It is also apparent, however, that without taking any action, the greenhouse effect will cause adverse environmental changes markedly affecting human life in the next few centuries.

Disposal of CO_2 into the deep ocean which is vast and highly unsaturated in CO_2 is considered to be one of the possible options (Nozaki 1991; Ohsumi 1995; Auerbach et al. 1996). This form of disposal may be only a temporary measure because the balance of CO_2 of the atmosphere and ocean will eventually equilibrate regardless of where in the oceans the CO_2 is originally discharged. Oceanic disposal, however, would reduce the atmospheric CO_2 concentration as the sea can retain considerable amounts (up to 70%) of the disposed CO_2 over a time scale of few centuries (Hoffert et al. 1979; Sorai et al. 1997).

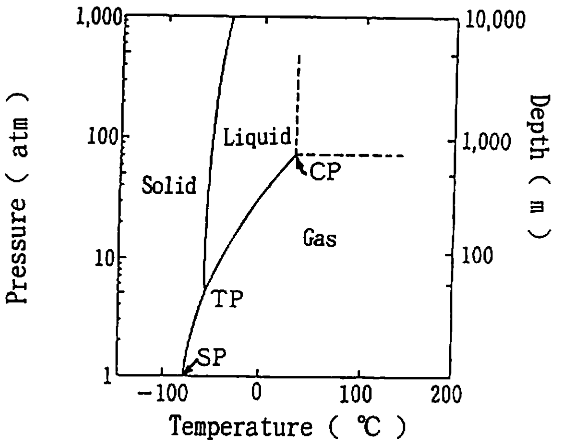

Fig. 1. Phase diagram of CO_2. SP means sublimation point (−78.5°C); TP, triple point (−56.6°C, 5.1 atm); CP, critical point (31.1°C, 72.9 atm).

CO_2 disposal in the deep sea will affect both directly and indirectly the marine ecosystem as a whole. In order to validate whether oceanic CO_2 disposal is acceptable or not, Omori et al. (1996) raised questions and discussed the possible immediate effects and uncertainties of injected CO_2 into the marine ecosystem. In the present review, we revise the previous paper with some further considerations, define the research needs to predict precisely the effects on deep-sea plankton and micronekton, and relate them to the overall concept of oceanic disposal.

Characteristics of CO_2 and Scenarios of Direct CO_2 Injection into the Ocean

Under pressures equivalent to a depth of approximately 500 m and at temperatures approximating those of the deep sea, pure CO_2 is a gaseous body, but at greater pressures becomes a liquid (Fig. 1). Under natural conditions, atmospheric CO_2 forms an aqueous solution, the concentration of the aqueous phase (CO_2 [aq]) being in equilibrium with the concentration of the atmospheric gaseous phase (CO_2 [g]). The concentration of the aqueous solution (CO_2 [aq]), however, can be greatly increased to form a "high CO_2 concentration seawater solution", and due to the increased density of this solution, scenarios to release such solutions at depths of 200–400 m and allowing gravity to form a plume sinking to an isopycnal stratum have been proposed (Haugan & Drange 1992). Pure liquid CO_2, if released at depths greater than 3000 m, its density is greater than the surrounding seawater and therefore, although affected by turbulent diffusion, it sinks and may be retained in topographic depressions (Marchetti 1977; Nakashiki 1996).

Oceanic disposal of CO_2 has been proposed and studied since the 1970s (e.g. Marchetti 1977; Hoffert et al. 1979). Concerning the technical aspects of disposal, several scenarios have been considered (Fig. 2). They are (1) releasing gaseous or liquid CO_2 into comparatively shallow fixed point from the coast by pipeline, (2) transporting liquid CO_2 to floating platforms in oceanic areas, and discharging it as liquid CO_2 into intermediate ocean depths from ships by means of a moving pipe, (3) dry ice dumping into intermediate water depths, (4) placement of liquid CO_2 in a restricted depression of the deep seafloor (Ohsumi 1995).

In the USA and western Europe, CO_2 release at depths of 500–1500 m by means of pipelines forming a droplet or dense plume, relying on rapid dispersion of CO_2 into the seawater from a point source (dispersion concept) have been seriously considered. On the other

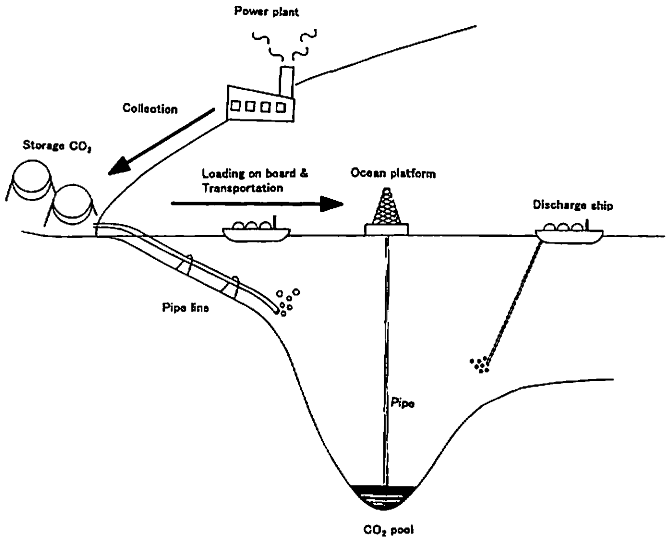

Fig. 2. Conceptual view of the various methods of CO_2 disposal in the ocean.

hand, in Japan, dry ice injection has previously been proposed, but more recently the feasibilities of depositing liquid CO_2 into a confined areas of the seafloor at depths of greater than 3000 m (storage concept) and CO_2 droplet injection to midwater from moving ships (dispersion concept) are being discussed (Nakashiki et al. 1991; Ohsumi 1995). We suggest that each of these methods presents potential environmental perturbations which will be critical to planktonic and benthic organisms around the site of disposal, however of different severities. This review outlines how injected CO_2 affects pelagic organisms and the concepts that require clear appraisal.

Ecology of Plankton and Micronekton in the Deep-Sea

The deep sea (depths greater than 1000 m) is a truely unique environment. If the various habitats of the world were compared, from the harsh variations in temperature and humidity of many terrestrial environments to the more moderate variations experienced in the environments of the seas, the deep sea would be shown to be an extreme example, having almost constant environmental conditions.

The deep sea is constantly dark, of near uniform temperature, showing little salinity variation and where currents occur of comparatively weak but consistent velocities. Deep-sea organisms, having evolved in such stable physical and chemical conditions, are unlikely to exhibit tolerance or resilience to changes in environmental characteristics beyond their normal ecophysiological experience.

There are several schemes of zonation proposed for pelagic organisms (cf. Hedgpeth 1957), but none have been universally accepted by all scientists working in this field. The primary reason is the lack of sufficient ecological information on which to base the effects of the physical gradients. The water layer between the surface and about 200 m is termed the epipelagic (photic) zone, and that between about 200 m to about 1000 m, the mesopelagic zone. The food web in the mesopelagic zone and below depends on the downwelling of productivity from the epipelagic zone with the exception of species dwelling around hydrothermal vents.

Biomass

Although the study of deep-sea organisms has attracted scientists since the early days of oceanography, the biomass of pelagic organisms throughout the water column still remains poorly known because of the difficulties involved in collecting samples. Information on the biomass is given in reports by Grice & Hulsemann (1965), Aizawa & Marumo (1967), Vinogradov (1968), Deevey & Brooks (1971), Angel & Baker (1982) and Kikuchi & Omori (1985).

Generally speaking, the biomass of zooplankton and micronekton at night is often largest at depths above 200 m (epipelagic zone), but it also increases at 500–1000 m. During the day, the largest biomass is often observed at 500–1000 m. Below 1000 m, there is a consistent trend for the biomass to decrease exponentially (Figs 3, 4).

The biomass sometimes increases in the layer immediately above the bottom of continental slope. This is due to the occurrence of benthopelagic species and the near-bottom concentra-

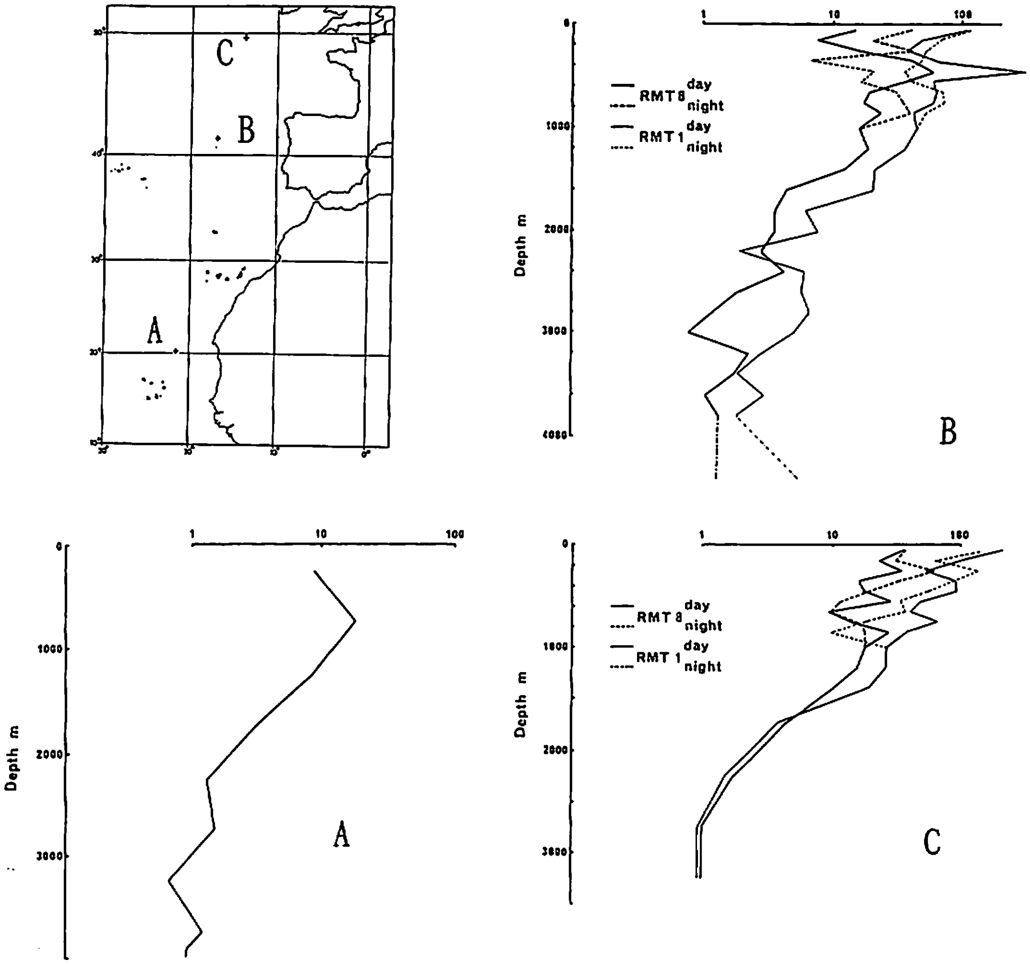

Fig. 3. Example of vertical profiles of biomass of plankton and micronekton at three stations A, B and C in the north-east Atlantic. Sampling gears used are RMT 1 and 8 (Roe & Shale 1979). The biomass is expressed as the displacement volume (ml) $1000\,m^{-3}$. *Dotted lines* on the profiles from position B indicate the values at 4300 to 4500 m where intermediate values were missing. After Angel & Baker (1982).

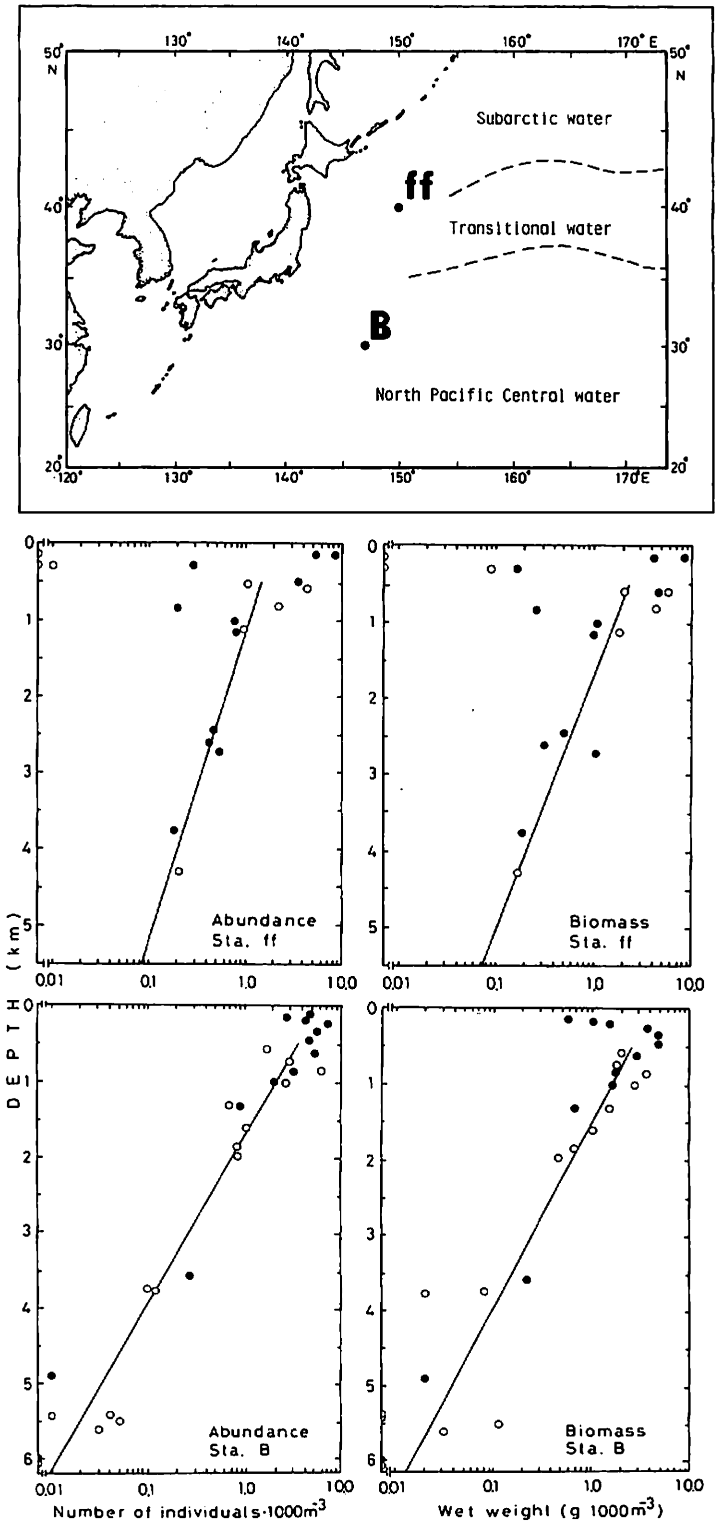

Fig. 4. Example of vertical profiles of abundance and biomass of pelagic shrimps at two stations, ff and B in the northeast Pacific. Sampling gear is KOC net (Anonymous 1980). The abundance is expressed as the number of individuals $1000\,m^{-3}$, and the biomass as wet weight (g) $1000\,m^{-3}$. *Open* and *closed circles* indicate day and night sampling depths, respectively. After Kikuchi & Omori (1985).

tion of diel vertical migrants during the daytime, and as a consequence of an enriched near-bottom environment.

The vertical distribution of zooplankton and micronekton, in general, is modified principally by the food supply, light penetration and temperature, although other physical variables such as salinity, dissolved oxygen and hydrostatic pressure are involved. The distribution of pelagic shrimp may be a good example (Omori 1974). As the distribution is affected by the depths where their food (copepods and mesoplankters) is available, in areas with low productivity the biomass of the shrimp is always large in the shallow layer, whereas a rich biomass extends deeper in areas with high productivity. In the subarctic waters, shrimp biomass gradually increases below 500 m, reaching a maximum at depths of 1000–3000 m (Vinogradov 1968). On the contrary, in low productivity tropical waters between 30°N and 10°N, the biomass is largest in the 200–500 m depth range and the pelagic shrimps gradually disappear around a depth of 1000 m (Kikuchi & Omori 1985).

Biodiversity

General features in marine biodiversity, in terms of species richness and evenness, are: (1) clear correlations between diversity and productivity are not observed, (2) high diversities are associated with the benthic rather than the pelagic realm, and (3) diversity is higher in coastal than oceanic areas (Angel 1993). Diversity of benthic species increases from polar seas to low latitudes, although the trend from the Antarctic to the tropics is less well established than that from the Arctic to the tropics (Clarke 1992; Kendall & Aschan 1993); it also tends to increase with increasing depth (Sanders 1968). These features suggest that more stable environments have a higher diversity. In pelagic communities, zones of high biodiversity are often found at the boundaries of biogeographical areas where different faunas mix. High diversities also result from the occurrence of many rare species. Rare species are a constant feature of open ocean pelagic communities, but because individual species often have very extensive geographical ranges, the total species richness of open ocean pelagic communities is far lower than that of coastal communities. The role of rare species in ocean pelagic communities remains to be fully understood. The question that needs to be raised is "do some rare species play more significant roles than others in the ecosystem of the habitat concerned?" (see Angel

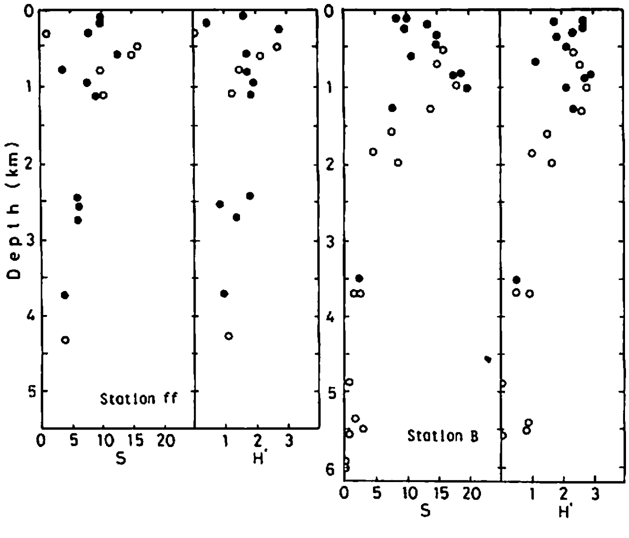

Fig. 5. Species richness (S) and species diversity (H') of pelagic shrimp in relation to depth at stations ff and B. *Open* and *closed circles* indicate day and night sampling depths, respectively. After Kikuchi & Omori (1985).

1992).

There are consistent trends for diversity of pelagic communities to increase with increasing depths down to 500–1000 m reaching to a maximum at about 1000-m depths (Fig. 5). Below this peak, there appears to be a sustained reduction in the diversity with increasing depth. Diversity sometimes increases again close to the bottom because of the occurrence of benthopelagic species (cf. Ohtsuka et al. 1993 for copepods). These species that inhabit close to the bottom, forming a link between the benthos and the water column, both quantitatively and qualitatively differ from the rest of the deep-sea plankton and may be important in the biological interactions within the benthic boundary layer (Wishner 1980), but still quantitative investigations are few.

Vertical migration

The water column down to about 1000 m is characterized by significant changes of the light field. Diel vertical migrations occur in the majority of epi- and mesopelagic species. Vertical migration patterns vary between species in the range over which they travel in the water column, and may be classified as a whole into a few representative patterns (cf. Omori 1974 for pelagic shrimp). These vertical migrations play an integral role in the fluxes of materials throughout the water column. Bathy- and abyssopelagic species living in complete darkness at depths greater than about 1000 m, however, do not show apparent diel migrations, suggesting the vertical transport of materials is much smaller than in the epi- and mesopelagic zones (Kikuchi & Omori 1985).

The depth of the sea bed has a strong effect on the range of diel migrants. Some epi- or mesopelagic species such as *Sergia lucens* and *Euphausia pacifica* are concentrated during the day in a layer close to the bottom in upper continental slope areas (Omori & Ohta 1981; Taki et al. 1996). Other dominant oceanic species such as *Sergestes arcticus* occur at depths of 800–1000 m in the water column during the day, but extend their range of vertical migration to depths of 1650 m on the continental slope and occur within 50 m of the bottom (Hargreaves et al. 1984). Many demersal fishes feed heavily on pelagic organisms occurring abundantly close to the bottom (e.g. Pereyra et al. 1969; Sedberry & Musick 1978). To advance beyond the descriptive basis of the variabilities of biomass and biological process, the behavioral characteristics of the dominant pelagic species should be sufficiently understood if the impact of possible CO_2 disposal is to be accurately assessed.

Some pelagic species perform marked ontogenetic or seasonal vertical migrations with periodicities of months. For example the copepod *Neocalanus cristatus*, one of the most abundant and important members of the zooplankton biomass in the Bering Sea and northern North Pacific, descends from the subsurface layer to 500–1000 m for overwintering and spawning (Miller et al. 1984). Their early life-cycle stages are spent in the upper food-rich euphotic zone. A further example is the Antarctic krill, *Euphausia superba*, a "key stone" species in the region. Their ontogenetic migration is different. Adults, which inhabit the euphotic zone, spawn heavy, yolk-rich eggs that sink to depths of 1000–2000 m prior to hatching (Mauchline & Fisher 1969; Ross & Quetin 1985). The larvae, during development, ascend swimming up to the epipelagic zone where they develop into the first feeding stage. The usual life cycle of bathypelagic species is for eggs to be yolk-rich and initially buoyant, and for the developing larvae to ascend to shallower layers as they undergo metamorphosis to the adult stage. Some species seem to either brood their progeny or have direct development.

Potential Impacts of CO_2 Disposal to Deep-Sea Organisms

Through evolutionary mechanisms, organisms show abilities to tolerate a certain degree of environmental fluctuation dependent on the environmental confines of the species in question, e.g., changes in the temperature, availability of food, variability of currents/wind speeds, etc. Similar arguments have been put forward for abilities to tolerate other stressors such as pollutants, and to mediate reproductive effort under high predation/fishing pressure, etc. (Battaglia & Bistol 1978). The deep sea experiences a far lower degree of fluctuation in environmental parameters than probably any other environment over recent (and probably ancient) geological time. Therefore, deep-sea organisms will probably have less genetic variance and a much lower ability to tolerate environmental fluctuations than neritic or epipelagic species. Quoting directly from Angel (1992, p. 34), "Thus mesopelagic and bathypelagic communities can be expected to contain the most highly tuned species with possibly the least tolerance of environmental change of all on earth". We think that this is a critical point in any assessment of the possible effects of CO_2 on the deep-sea environment.

Although seawater is a very strong buffer, the suggested levels of CO_2 discharge will affect the pH of a volume of water. The degree and distribution of the affected water depending on both the method of discharge and the degree of diffusive mixing and turbulance of the water into which the discharge occurs. As of yet, although there is only limited data on the effects of pH for certain neritic marine species; data for deep-sea species is negligible. The possible combined effects of reduced pH and high pressures may further affect the speciation of metal ions. Particulate organic matter absorbs many metal elements in the marine environment making the ions chemically inert, but by lowering the pH this equilibrium may be synergistically altered.

The impact of lowered pH to aquatic organisms is sometimes judged by a percentage mortality of adult forms using isomortality curves, but such crude forms of toxicity testing assess only acute levels as a criteria for the judgment of safety. Sub-lethal effects on reproduction, growth, metabolic rates and longevity may be experienced with smaller decreases in pH. Although the stressors may not necessarily kill the organisms directly, the long term chronic effects may have equally drastic results and subsequently affect the whole ecosystem. Precise information about the effect of lowered pH not only on single stage but over the entire life cycle of various deep-sea pelagic species, particularly those utilizing calcium carbonate in their bodies such as mollusks, foraminiferans and echinoderms, is essential for modeling impacts.

For epipelagic oceanic zooplankton species including *Neocalanus cristatus*, *Eucalanus bungii bungii*, *Metridia pacifica*, and *Sagitta elegans* maintained in seawater of which the pH was lowered by the addition of HCl, lethal pH levels (50% mortality) has been evaluated in the range of 4.8 to 5.9 over a 24-h exposure and 5.0 to 6.7 for a 72-h exposure (Yamada & Ikeda, forthcoming). The physiology of the metabolism underlying the life processes of deep-sea species is still largely unknown. Meso- and bathypelagic organisms may be more sensitive to raised CO_2 and lowered pH than epipelagic ones, but Pörtner & Reipschläger (1996) suggested that because deep-sea fish lead a sluggish mode of life the effect of CO_2 for them will be less than for shallow living fish. They argue that the magnitude of the Bohr effect depends upon the level of activity and will, therefore, be smaller in deep-sea pelagic organisms. Lowered pH is known to reduce the oxygen affinity of haemoglobin or hemocyanin (see Prosser 1973, p. 213–215) but the magnitude of alteration of this Bohr effect by pH on deep-sea plankton and micronekton has not been examined so far. Perhaps, the best information about blood chemistry currently available is that for hydrothermal vent animals (Childress & Fisher 1992).

In pathways linking deep-sea organisms with the productive upper layers, the behavior of "marine snow" consisting of loose aggregates of living and non-living particles such as faecal pellets and chitinous molts bound together by mucus should be considered (Alldredge & Silver 1988). As they sink, the marine snow is extensively re-packaged by being fed upon by plankton and micronekton and undergoing microbial degradation. The re-packaging process, however, declines with depth, and presumably the marine snow finally reaches the seafloor and is taken in the sedimentation processes. Several effects on bacteria, which play a significant role in the re-packaging process and re-cycling of organic carbon, by an increased partial pressure of CO_2 have been determined (see Dixon & Kell 1989). The effects include, for example, blockages of the bacteria's enzymic decarboxylation pathways, changes in the function of cell membranes, etc. Depending on the depth and location of the CO_2 injection, there is the possibility that more marine snow and flux of dead organisms may accumulate on the seafloor with a very slow degradation rate, potentially leading to anaerobic conditions in the sediments. The influence of any chances in the activity of marine bacteria on the deep-sea food web remains to be investigated.

Perception and behavioral responses of deep-sea zooplankton and micronekton to CO_2 plumes are not known. In the plume scenarios outlined in Auerbach et al. (1996), effects will be most critical on the surrounding physical characteristics of the seawater layer into which the CO_2 enters; even lowering by 1°C may cause an effective thermal barrier to organisms. The effect of such horizontal physical/thermal barriers and/or layers with different chemical properties may disrupt the "ladder" style migration pattern of many pelagic organisms which will not pass through a barrier if sensed (see Omori et al. 1994).

Some Suggestions on Research Requirements and Conclusion

It is still extremely difficult to maintain and experiment on deep-sea plankton and micronekton in the laboratory in conditions representative of their natural ones. Therefore, many species will have to be experimented on in the sea. Submersibles and remote observation vehicles may be indispensable for direct observations of the response of deep-sea plankton and micronekton to lowered temperature and/or pH of simulated CO_2 plumes and for sampling specimens. Collection of the specimens in good condition for experimental studies requires further technological development. To detail the physiological effects of increasing partial pressures of CO_2 disposal in the laboratory, construction of pressurized culturing facilities are essential, but this may not be difficult with modern technology, if only adequately funded.

Without such facilities, however, some preliminary information on the effects of pH on the hatching success and early development may be gained at in situ deep-sea temperatures but under 1 atm (i.e. normal laboratory conditions) using fertilized eggs of deep-sea zooplankton collected in the field. At sampling sites where the vertical temperature gradient is steep, the only specialized gear needed for this type of experiment is a net equipped with a thermally protected codend to recover live specimens, as developed by Childress et al. (1978). Childress & Price (1983) maintained the bathypelagic mysid *Gnathophausia ingens* in a land-based laboratory for an extended period. However, where the vertical temperature gradient is very small (i.e. polar seas), such gear is not required for experiments. Successful hatching of eggs and larval development have been reported for the mesopelagic ostracod *Conchoecia pseudodiscophora* (Ikeda 1992) and the copepod *Paraeuchaeta elongata* (Ikeda and Hirakawa 1996) in the Japan Sea. For the vertically migrating myctophid *Benthosema pterotum*, Gjøsaeter & Tilseth (1988) were able to obtain larvae by artificial fertilization using ripe gonads of males and females on board the ship. It should be noted, however, that parallel experiments at in situ hydrostatic pressures are essential to validate any results at 1 atm, as physiological effects of increased partial pressure of CO_2 may vary with pressure.

Any experiments should preferably be carried out using several combinations of different CO_2 concentrations, pHs, other physical properties and exposure times. Schöne (1962) and Vernberg (1972) reviewed the effects of CO_2 on the activity/behavior and metabolism of aquatic crustaceans. According to them, *Daphnia*, *Palaemonetes*, *Crangon* and some other crustaceans swim upward in relation to gravity and light when exposed to increased partial pressure of CO_2 and in another crustacean *Squilla mantis*, CO_2 accelerates respiratory movements of abdominal appendages.

Scenarios for the ocean disposal of CO_2 suggest the effects to occur in a limited area around the point of release, however, the possible effects of a boundary layer of even slightly different physical or chemical properties dissipating away from the release point on the behavior of marine organisms is critical as to whether the deep sea will be an optimal site for disposal. The severity of the near-field impact, and presumably the far-field impact too, may be minimized by the careful selection of sites for CO_2 release. In order to access the suitability of sites, however, more details regarding the vertical distribution of zooplankton and micronekton in different waters and the behavior, physiology and toxicology of these organisms are clearly needed.

Considering the biomass and biodiversity of plankton and micronekton, environmental processes and the potential for the exploitation of living resources, our opinion is that CO_2 discharges at depths shallower than 1000 m should be avoided in order to minimize the effects on the biological processes in the upper water column. Maximum species diversity occurs about 1000 m for pelagic organisms and, according to Rey (1983), 2000–3000 m for benthic assemblages. In the water column deeper than 1000 m, on the current information available, the number of species that undergo extensive vertical migrations appears to be low. The biomass of plankton and micronekton rapidly decline and links between the epipelagic zone and the deep sea become progressively more tenuous with increasing depth. The effect of any disturbance at depths of 2000–3000 m or greater is not likely to extend to the epipelagic zone at significant rates via biological pathways. Given these features of the deep sea, it can be concluded that the deep sea is a sink for materials rather than a source. As referred by Angel & Rice (1996), this has been well demonstrated by studies of the impact of a low level radioactive damping sites in the north-east Atlantic where isotopes from the damping sites were not found in organisms in the overlying water column (Feldt et al. 1981).

Assessments of the effect of ocean CO_2 disposal should not be made unless sufficient data is available to answer various questions. Particularly of concern is the misuse of the limited biological data available at present, to justify the feasibility of engineering projects. Unambiguous, systematic analysis of the potential effects CO_2 disposal on the biota are clearly imperative. From a biological point of view, considering the possibility of CO_2 discharge and of CO_2 retrieval if necessary, confined release of CO_2 in restricted depressions of the seafloor at depths greater than 3000 m seems to be preferable to dispersion in midwater. However if dispersion methods are to be considered, the development of more refined technological solutions to increase the rate of dispersion of CO_2 from a point source and therefore result in a smaller pH reduction should be emphasized.

Large-scale field experiments, ideally a few tenths of the size of a full industrial disposal, are advisable for empirical proof of assessment of effects and also for the improvement of the modeling at several carefully selected locations and depths. The local oceanography at the actual selected sites for experimental CO_2 discharge should be clearly assessed well in advance, and the species composition as well as the biomass determined, so that the most important factors and parameters which may affect the deep-sea ecosystem can be identified before starting any field experiments.

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