Role of the marine biosphere in the global carbon cycle

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Abstract
The geochemical disequilibrium of our planet is due mainly to carbon sequestration by marine organisms over geological time. Changes in atmospheric CO₂ during interglacial-glacial transitions require biological sequestration of carbon in the oceans. Nutrient-limited export flux from new production in surface waters is the key process in this sequestration. The most common model for export flux ignores potentially important nutrient sources and export mechanisms. Export flux occurs as a result of biological processes whose complexity appears not to be accommodated by the principal classes of simulation models, this being especially true for food webs dominated by single-celled protists whose trophic function is more dispersed than among the multicelled metazoa. The fashionable question concerning a hypothetical “missing sink” for CO₂ emissions is unanswerable because of imprecision in our knowledge of critical flux rates. This question also diverts attention from more relevant studies of how the biological pump may be perturbed by climatic consequences of CO₂ emissions. Under available scenarios for climate change, such responses may seem more likely to reinforce, rather than mitigate, the rate of increase of atmospheric CO₂.

There are other ways of saying it, but really the most urgent question for biological oceanography is whether the marine biosphere will mitigate or reinforce the increase of anthropogenic greenhouse gases in the atmosphere. This increase, as Fig. 1 shows, is an instantaneous step function on the time scale of natural changes of similar magnitude.
A simple probe of the gross chemistry of the atmosphere, ocean, and sediments would reveal a state of geochemical disequilibrium. A reactive gas, oxygen, is abundant in both atmosphere and ocean, and carbon (with which it would combine on a lifeless but watery planet) is largely sequestered in biogenic carbonate formed below or along the margins of oceans. This geochemical disequilibrium must be maintained by biological processes against a background of geological episodes of subduction and volcanism, during which C is cycled between biogenic carbonate rocks and the atmosphere (Owen and Rea 1985; Volk 1989).

Our probe might not sense the critical fact that the biologically mediated flux that maintains the geochemical disequilibrium is small compared with the transfer of CO₂ across the ocean surface driven simply by diffusion and solubility. Figure 2 shows a new version of a familiar figure to make this point. We would surely see that the surface layer of the oceans is in equilibrium with the atmosphere, while the deeper water masses are oversaturated with dissolved CO₂. From this we draw the basic concept of the “biological pump”: downward flux of C is maintained by gravitational settling of organic and carbonate C, fixed autotrophically in the surface layer by plant cells. We

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assume that this flux is constrained by the supply of a limiting nutrient, usually supposed to be inorganic N as NO₃.

To predict the response of the ocean (and its biological pump) to a step function in the radiatively active gases in the atmosphere is difficult or even impossible, given our uncertainties about relevant processes and rates. Paradoxically, we are more confident about the role of marine biota in the remote past than in the present perturbation and, by constraining our predictions, this knowledge may help us to predict the role of marine biota in the immediate future (Berger et al. 1989).

**Biogeochemical evolution of the primitive atmosphere**

The CO₂-rich atmosphere of the Proterozoic was progressively modified by the sequestration of C in carbonate rocks and organic sediments by stromatolite-building and other cyanobacteria (Rothschild and Mancinelli 1990) in shallow seas. By the early Cambrian, sufficient free oxygen was available both to oxidize reactive elements in the rocks (e.g. Fe to Fe oxides) and to produce a surplus sufficient for the evolution of protists and metazoa.

The geochemical consequences of marine productivity dominate the geological record: terrestrial plants have endowed us with only 3–7 × 10³ Gt C of coal, compared with 40 × 10⁶ Gt C of carbonate rocks from marine biota. However, the pCO₂ atm decline over the 60 × 10⁶ yr from the Cretaceous to the Pleistocene may be due to the activity of land plants. If the Cretaceous atmosphere resulted from active sea-floor spreading and vulcanism, and if Cretaceous oceanic circulation was as active as today (Manabe and Wetherald 1980), the subsequent decrease in pCO₂ atm may have been due to the evolution of angiosperm forests (Volk 1989c). If, on the other hand, the CO₂-rich Cretaceous atmosphere originated in weak oceanic circulation and low plankton productivity, strengthening circulation and increasing marine productivity may have progressively reduced pCO₂ atm to Pleistocene levels.

**Role of the biosphere in Pleistocene glacial transitions**—Because the rate of change in pCO₂ atm during Pleistocene glaciation-interglacial transitions approaches our scale of interest, it may be profitable to examine how small changes in solar forcing (Berger et al. 1990) could be so amplified by changes in pCO₂ atm as to mediate transitions between glacial and interglacial climates (Genthe et al. 1987). Perhaps such a process might also amplify or reduce the effects of anthropogenic forcing of climate change in the coming centuries.
A cornucopia of scenarios, having a rapid replacement rate, purports to explain such changes in $pCO_2$ atm and also the concomitant changes in terrestrial biosphere C; the sum of these two fluxes must have been absorbed by (or released from) the oceans during a glacial transition. It is generally supposed that the marine biosphere was in some way implicated (e.g. Barnola et al. 1987; Berger et al. 1987).

At glacial onset, a flux of 93–1,350 Gt C from terrestrial plants, litter, and soil occurred (Faure 1990), to which must be added 211 Gt C from the atmosphere (to reduce it from 280 to 180 ppm), thus requiring a sink in the ocean of 304–1,561 Gt C to maintain global balance. This amount is within observational constraints, for Sarnthein et al. (1988) computed a return of 580–720 Gt C from the ocean to the atmosphere during the transition to our own interglacial period.

In recent years, thinking on these fluxes has evolved rapidly. From reliance on the
relationship between ocean temperature and $p$CO$_2$-ocean (e.g. Broecker 1982), recent scena-
arios are more likely to invoke increased ocean productivity during glaciations to draw down $p$CO$_2$-atm. Candidate mecha-
nisms have ranged from increased produc-
tion of biogenic carbonate by corals (Berger 1982), through changes in the Redfield ratio of sinking material (Broecker and Peng 1982; Broecker and Takahashi 1984) to increased nutrient supply from continental shelves ex-
posed during glaciations (McElroy 1983; Broecker and Peng 1984; Walsh 1988). Cur-
rent thinking, however, converges on the effects of altered ocean circulation on the supply of nutrients to the photic zone, es-
pecially in low latitudes where most new production occurs (Barber and Chavez 1986), but perhaps not in the Arabian Sea monsoon region (Sarkar et al. 1990). Sedim-
ent cores suggest that during Pleistocene glaciations the ocean was characterized by stronger upwelling centers (Muller and Suess 1979; Boyle 1986; Mix 1989a), while sub-
tropical gyres were more stratified and less productive (Sarnthein et al. 1987; Sarnthein and Wann 1990). Such data suggest 38% more productivity at low latitudes in the Atlantic (Mix 1989b), as well as an increase in the tropical Pacific (Pedersen et al. 1988), for a significant increase globally (Sarnthein and Fenner 1988).

Other scenarios have emphasized high-
latitude processes. In the North Atlantic, as the polar front approached the meteorological intertropical convergence zone, increased wind stress would favor pulsed pro-
duction and export flux, resulting in a drawdown of $p$CO$_2$-atm. At the same time, formation of deep water masses may have ceased at high latitudes in the North Atlan-
tic (Oppo and Fairbanks 1987), with con-
sequences for Southern Ocean alkalinity and photic zone NO$_3$ and SiO$_3$ (Sarmiento and Toggweiler 1984; Broecker and Peng 1989; Knox and McElroy 1984).

It has also been suggested that plant growth in our present interglacial Southern Ocean may be Fe-limited because of low aeolian input of this element, a flux thought to have been greater during glaciations (Martin and Fitzwater 1988; Martin 1990) though sediment cores suggest reduced, rather than enhanced, export flux in Ant-
arctic seas during glaciations (Boyle 1988; Mortlock et al. 1991). The question of the role of Fe in the Southern Ocean is, of course, one of the central subjects of this sympo-
iwm.

Mechanism of the biological pump—For simplicity, we might characterize the bio-
logical pump as having three components, each representing a different ecological pro-
cess: a rotary pump which circulates mate-
rial in the microplankton food web of the photic zone, an Archimedian pump by which flux of fecal and aggregated material occurs continually under gravity, and a reciprocating pump by which diel migrants actively carry material down at dawn, to rise again at dusk to feed.

The usual concept of the biological pump does not accommodate the consequences of the complex interactions between plant growth and the alkalinity of seawater for flux of CO$_2$ across the sea surface. Further, it usually simply assumes that sinking flux of POC is a measure of the rate of NO$_3$-driven production in the photic zone. Al-
though this balance may be confirmed by $^{15}$N uptake measurements (e.g. Knauer et al. 1990), the simple model ignores active flux of DON and respiratory C by diel mi-
gnants, vertical advection and diffusion of DOM, and variable organic-inorganic C and C:N:P ratios of the flux.

These omissions have had an important impact on our thinking. Many (most?) bi-
ological oceanographers would probably still accept the simple paradigm that weakened equatorial upwelling should reduce the bi-
ological uptake of C and thus enhance the normal rate of CO$_2$ outgassing there. Con-
versely, most might be surprised at the con-
comitant concept that reduced upwelling of CO$_2$-rich water would actually result in re-
duced outgassing of CO$_2$ from a warmer-
than-normal surface water (e.g. Siegenthaler and Wenk 1984). Actually, it must be the balance between these two processes that determines flux across the sea surface.

Nutrient sources and carbon sinks—In simple models, photosynthesis is the only autochtonous source of particulate C and the limiting nutrient is usually supplied in our models only by eddy flux from below, although diverse intermittent mechanisms (Gargett 1991) should also be accommo-
dated: wind- or buoyancy-driven winter overturn, seasonal upwelling driven by non-linear local or remote forcing, cross-shelf eddy transfer (e.g. Houghton et al. 1987), event-scale wind mixing (Eppley and Renger 1988), vorticity induced by eddy shear (Pollard and Regier 1990), wind-stress curl, and isopycnal upwelling. Only by invoking all such mechanisms can we explain the spatial variability of sea-surface chlorophyll.

The concept of a single source of fixed N may not be sustained much longer. The supply of fixed N by the cyanobacteria *Trichodesmium* is likely to be an important source of export flux, regionally perhaps comparable to NO$_3$-driven production, and representing true net sequestration of CO$_2$ (Bird pers. comm.). Dense blooms of *Trichodesmium* are widespread in moderate latitudes and supply fixed N at rates significant relative to algal demand and sometimes more rapidly than NO$_3$ is supplied by vertical mixing (Carpenter et al. unpubl.; Karl unpubl.). Further, the endosymbiotic cyanophyte *Richelia* releases fixed N to sustain diatom blooms in central gyral waters (Verrick 1974) and may also be a significant source of N.

Also usually ignored is atmospheric deposition, especially leeward of continental masses. On the eastern continental shelf of North America, this may contribute 20–30% of biologically available N (Paerl et al. 1990). Although Legendre and Gosselin (1989) recently calculated that aeolian input of NH$_3$ in the North Atlantic could exceed upward transport of NO$_3$ by a factor of three or more, this has now been shown to be incorrect, and ~10% is more likely (Laws 1991; Galloway et al. 1985). Nor can we ignore isopycnal advection of properties, since variability of plankton abundance in the California Current (and perhaps other eastern boundary currents) is principally determined by the variable transport of nutrient-rich water from higher latitudes, not by local coastal upwelling (Bernal and McGowan 1981). The simple concept of the biological pump does not acknowledge vertical advection of dissolved organic matter. If the inverse, linear relationship between NO$_3$ and DON in the upper kilometer observed by Sugimura and Suzuki (1988) is correct, then downward mixing of DON (and DOC) must be an important component of the export flux from the photic zone (Toggweiler 1989).

We also need to know how much of the total annual particle flux for each ocean basin comprises seasonal or intermittent blooms which may sink almost directly to the sediments. Such flux is caused by rapid growth of diatoms outstripping the capacity of herbivore consumption (Riemann 1989; Lampitt 1985; Prézelin and Allerdredge 1983; Takahashi 1986; Nair et al. 1989) or else by the rapid development of salp populations capable of consuming the standing crop of small cells and producing rapidly sinking fecal material (Bathmann 1988; Wiebe et al. 1979).

Finally, we must separate flux from micro- and mesoplanktonic food webs (Michaels and Silver 1988). Microplankton produce relatively small fecal material, including abundant minipellets from protists (Gowing and Silver 1985) with low rates of sinking, and even more abundant submicron particles from flagellates (Koike et al. 1990). On the other hand, mesoplankton produce larger, faster sinking fecal material and also interzonal diel migrants may actively transport material downward (Longhurst and Harrison 1989).

**Balance between micro- and mesoplankton consumption of primary production**—Classically, mesoplankton were thought to dominate grazing of phytoplankton, but actually they rarely consume more than a small fraction of daily primary production.

Since the relative size of phytoplankton cells is progressively smaller offshore and toward low latitudes, grazers must follow the same trend. Mesoplankton consumption in oceanic situations is almost always <20% of daily production (Tsuda et al. 1989). In intermittent upwelling systems, as off Peru, open-ocean consumption by mesozooplankton may be that low (3–8%, Dagg et al. 1980). During the JGOS 1989 North Atlantic spring bloom study, mesoplankton removed only 1–2% of the daily primary production (Morales et al. 1991). Of course, at the end of any algal bloom, consumption may briefly exceed production.

In shallow shelf seas, mesozooplankton consumption is somewhat higher than in the open ocean, usually 10–40% of daily
production (Dagg et al. 1982; Chervin et al. 1981; Pace et al. 1987; Longhurst 1983) but may approach a balance with primary production, as in Puget Sound (60–70% daily, Welschmeyer and Lorenzen 1985a,b), or even exceed it, as in summer in the Celtic Sea (Joint and Williams 1985). Oceanic microplankton, on the other hand, frequently consume 70–90% of daily primary production (Welschmeyer and Lorenzen 1985a).

In coastal and high latitudes, experiments return quantities usually between 10 and 50% of standing stock or 25–100% of potential production daily (Gifford 1988; Paranjape 1987, 1990; Burkill et al. 1987).

Role of mesoplankton in particulate export flux—If mesoplankton are not the principal consumers we thought in the past, what is the importance of their apparently fast-sinking fecal material in oceanic export flux? Can we relate this material directly to new production as the biological pump concept requires (e.g. Michaels and Silver 1988), since mesoplankton fecal pellets will usually not represent more than a small fraction of the total consumption in the overlying photic zone?

The concept that sinking fecal pellets contribute to vertical flux dates from Lohmann (1902) and is confirmed by many trap observations (e.g. Lorenzen and Welschmeyer 1983; Sasaki et al. unpubl.), but some anomalous observations compel our attention: crustacean fecal pellets having sinking rates that should take them to the bottom may instead be consumed or broken up by other organisms while held in suspension by vertical turbulence in coastal areas (Smetacek 1980); there is also a remarkably close similarity between open-ocean profiles of pellets and of copepods, suggesting little or no vertical pellet flux (Krause 1981; Bathmann et al. 1987). A similar case can be made for profiles of crustacean exuviae (Sakamoto 1986; Longhurst et al. 1984).

Depth profiles of POC production and consumption—The biological pump is usually modeled as flux between two boxes: a surface photosynthetic and a deep aphotic box where sinking C is respired and NO₃ regenerated. Whether this geochemical shorthand is supportable can be determined only from a knowledge of the profiles of light, temperature, nutrients, primary production, heterotrophic respiration, and sources of POC. Because profile characteristics are determined principally by physical processes, we can generalize plankton profiles for regions of the ocean having characteristic profiles for density (Fig. 3).

Depths of maximum algal and growth rate coincide when these are shallow but are progressively separated in profiles where the maxima are deeper. In such cases, the depth of maximum productivity is shallower than the chlorophyll maximum, which lies at or just above the nutricline (Cullen 1982; Longhurst and Harrison 1989). Heterotrophic bacterial biomass follows algal biomass and productivity, reflecting the utilization of DOM released directly from plant cells and heterotrophs (Sherr and Sherr 1988).

New observations of oceanic DOM profiles (Sugimura and Suzuki 1988) show steep, biologically driven gradients to ~500 m, raising the possibility of a flux-driven connection between the “zooplankton remineralization loop” discussed by Banse (1990a) and the microbial loop of the photic zone. From the depth distribution of trophic groups of mesoplankton we can conclude at what depths fecal POC, excretory DOC, and respiratory C are released and at what depths different fractions of POC are consumed (Fig. 4); results are consistent with most particle flux from the photic zone being consumed and remineralized within the subsequent 200–300 m (e.g. Martin et al. 1987; Bishop et al. 1986).

Active export flux by vertical migrants—Diel migrations, both within the photic zone and between the photic zone and the mesopelagial, have been well described so we can predict which genera will participate in each kind of migration (Fig. 5). Diel migration in coastal and seasonal situations can be considered modifications of the open-ocean paradigm. Why diel migration should occur was a Holy Grail for planktologists for many decades. Only recently have we begun to ask, rather, what are its consequences for vertical flux of material? (e.g. Longhurst et al. 1989, 1990; Longhurst and Harrison 1988, 1989). Interzonal migrants feed in the photic zone at night and rest in colder, dark water by day at 300–800 m.
The guts of copepods, which are usually ~70% of these migrants, are emptied prior to, or early in, their descent. The gut contents of only the larger nektobanks are carried down with them. Both plankton and nektobanks release respiratory C and excretory NH₄ at depth, usually at 400–600 m. Their feeding pattern ensures that this dissolved material originates in the surface layers.

At seven stations in low latitudes (Longhurst et al. 1990), the mean flux of respiratory C from diel migration was equivalent to ~30% of sinking flux across the thermocline. From the global biomass of zooplankton in regions where diel migration is significant, respiratory flux is 0.14–0.27 Gt C yr⁻¹, which is 8–17% of Sundquist's (1985) estimate for total sinking flux of C at 200 m between these latitudes, extrapolated from Betzer et al. (1984). To this must be added the flux from gut contents of nektobanks and the loss of C (by respiration and predation) from populations of deep over-wintering oceanic copepods. Work in progress in the North Atlantic suggests that two-thirds of the migrating biomass do not survive the winter and represent active transport from the photic zone to depths of ~600–800 m. The comparable flux of metabolic nitrogen as NH₄ downward out of the photic zone as a result of diel migration requires upward revision of the f-ratio (relating NO₃-driven to
total production) of from 5 to 65%; the relation between N flux due to diel migrants and sinking particle flux is positively correlated with the depth of the mixed layer (Longhurst et al. 1989), the ratio being 10% for mixed layers 40–50 m deep and 20% at 110–120 m.

**Balance between production-consumption: Excess nutrients**—If we are to understand high NO₃, low chlorophyll (HNLC) regions, we must be able to quantify the balance between photosynthesis and consumption, both regionally and seasonally. Seasonally pulsed production of phytoplankton, exceeding the consuming capacity of herbivores (e.g. Billet et al. 1983), is easily observed, but herbivore constraint on the numerical growth of plant cells is harder to demonstrate. In grazing-constrained HNLC situations, we might expect to find unusually high pheopigment : chlorophyll ratios (Thomas 1979), especially where metazoan grazers are abundant. Although the dynamics of pheopigments in the water column are complex (reingestion, photodegradation), these processes should not differ significantly in normal and in HNLC regions.

The HNLC region of the eastern tropical
Pacific lies consistently to the south of the equator in the EASTROPAC data, but mesoplankton biomass, chlorophyll, and pheopigments all take their highest values along or to the north of the equator. The Pheo: Chl a ratio is close to unity over the whole region (Thomas 1979; Beers and Stewart 1971), suggesting that the NO3 anomaly does not result from mesoplankton grazing pressure. Further, a meridional section across the region (Chavez et al. 1990) shows no correlation between microheterotroph abundance and surface NO3, an earlier meridional section of protist abundance (Beers and Stewart 1971) does show higher abundance at some stations south of the equator, but this is not a clear result. Thus, neither meso- nor microheterotroph abundance is unequivocally associated with high near-surface NO3 in available observational data, so suggestions that the anomaly is due to grazing constraint (e.g. Toggweiler 1990) are not supported by the EASTROPAC data. The same conclusion was reached by Thomas (1979) for the region where superficial HNLC water is advected from the distant coastal upwelling region, rather than originating in equatorial upwelling.

Models for C flux analysis

Two generalizations are available for models of the marine biosphere: by simple network analysis to a few interacting biotic compartments (e.g. Volk and Hoffert 1985; Fasham et al. 1990), and by allometric arguments to size-scaled linear biomass spectra (e.g. Platt 1985; Echevarria et al. 1990). Such models are capable of delivering output within observational constraints, although it is difficult to be sure that they do so for the right reasons, and the arguments that follow suggest that most currently used models actually simulate trophic functions dispersed among taxa, rather than the purported function-specific taxonomic units. Because such models seem to work, we must assume that our generalizations about biological processes are sufficiently robust to deliver realistic output despite inappropriate assumptions concerning the nature of the simulated compartments.

Nevertheless, these two main classes of models require simplifications that cannot be supported by ecological analysis and we must ask to what extent their output is really reliable. The basic assumption for size-scaled models is that material passes in a linear fashion from small to large biota and for network analysis that biota can be arranged into a few compartments, comprising subsets of zooplankton, phytoplankton, and bacteria. The consequences of modeling all metazoan biota as just a few interacting compartments are difficult enough to predict, even though functional feeding groups can be identified for mesoplankton, as we have discussed above. But what of the protist plankton, the principal photic zone consumers? Can we treat them as reducible to a few feeding groups like metazoa?

Network models: Dispersed autotrophy and heterotrophy among protists — Although bacteria and protists are the major component of respiration in the ocean, we are only now learning that to compartmentalize their trophic functions involves uncertainties that are much greater than for metazoa because the functions of photosynthesis, predation, and heterotrophy are dispersed among all protist groups, and many individual cells frequently perform more than one of these functions. It is now apparent that all groups of functionally photosynthetic “algae” include forms (sometimes abundant) that also attack and consume other protists: diatoms appear to be the only exceptional group. Conversely, most groups of “heterotrophic” protists, with the possible exception of tintinnids, also include abundant forms which harbor photosynthetic symbiotic algal cells or photosynthetic plastids.

Thus, the classical distinction between protozoa and algae is no longer tenable (Sleigh 1991), and we should abandon this misleading classification. However, our ecological interpretation of function among protists must be sensitive to the Great Divide between procaryotes (metabolically diverse and adaptable to changing ambient chemistry through DNA recombination by plasmid exchange) and eucaryotes (structurally diverse but metabolically less flexible through DNA exchange at gametogenesis).

The autotrophic symbionts accommodated by “protozoan” taxa whose dimensions permit such a relationship are diverse:
cyanobacteria, chrysomonads, prymnesiomonads, cryptomonads, and dinoflagellates (Taylor 1987). To further complicate the issue, heterotrophic dinoflagellates may themselves harbor symbionts, using a variety of mechanisms to do so. Symbionts may or may not dominate the physiology of the host by an exchange of molecules partly satisfying the nutrient demands of both symbiont and host. The opposite case, of chlorophyll-bearing, “phytoplanktonic” protists that regularly consume other living cells, is also widespread. The dinoflagellate genus Ceratium is a classical component of autumnal blooms and of the oceanic phytoplankton, yet includes species capable of consuming diatoms larger than themselves, with a variety of engulfing mechanisms (Taylor 1989). The same is true for the small, abundant genus Protoperidinium, which is capable of daily consuming >20 large diatom cells to support a growth rate of 1.7 divisions daily (Jacobsen 1987).

Many genera of nanophytoflagellates (including coccolithophores) ingest bacteria by a variety of techniques. These chlorophyll-bearing flagellates are among the principal consumers of bacteria in lakes (Bird and Kalff 1986) and in the marine pelagial (D. F. Bird pers. comm.). In the Sargasso Sea, phagotrophic (mixotrophic) nanoflagellates may constitute 50% of all photosynthetic nanoplanckton and contribute significantly to consumption of bacteria (Caron and Lim unpubl.).

Our knowledge of predatory “protozoa” and photosynthetic “protozoa” is quite insufficient to generalize their effect on our measurements of (for example) heterotroph respiration or size-fractioned photosynthesis. Plastid-bearing ciliates in both neritic and oceanic environments may represent significant proportions of large cell photosynthesis, reaching ~25% in both temperate and Arctic environments. Even so, because of their fragility on polycarbonate filters, the ciliate fraction of the large-cell component of size-fractioned photosynthesis may be underestimated (Putt 1990).

The functional complexity of the pelagic protistan ecosystem approaches the spatial and functional complexity of coral reef organisms within their carbonate matrix. The protist ecosystem exists in a high viscosity matrix which permits spatial complexity through the development of microzones within which single protist cells interact chemically with ambient organic and inorganic molecules. Their symbionts and the bacteria associated with their cell wall share their microzone and participate in its chemistry. The complexity of this part of the biosphere stems also from the interaction within it between the metabolically labile procaryotes, the metabolically complex eu- caryotes, and the structurally diverse small metazoa (Longhurst 1990).

Attempts to simplify and compartmentalize even the major trophic relationships in this protistan ecosystem result in complex networks (Fig. 6), which recall the unstructured food-web model of Isaacs (1972). As discussed by Banse (1990b), the complexity of metazoan food webs may be more apparent than real, but it is perhaps in the protistan food web, if anywhere, that we can expect to find a lack of biomagnification because of the complexity of trophic links.

Biomass spectrum models: Variability of predator-prey ratios—Though size-scaled plankton biomass spectra usually have a slope close to that predicted by allometric models, it is only recently that they have been made to accommodate events such as loss from the linear biomass spectrum, which occurs during a spring bloom when autotrophic production overwhelms the capacity for consumption of the relevant larger size classes and algal cells sink unconsumed (e.g. Rodriguez et al. 1987). Further assumptions concerning the relative sizes of predators and prey are inherent in linear biomass models. A prey-predator linear ratio approaching what is often (but probably incorrectly) assumed for terrestrial ecosystems is also proposed for marine biota (e.g. Fenchel 1988). Available generalizations suffer the same defect as classical terrestrial models, only more acutely: this ratio fits chase-and-grab predators (hawks-sparrrows, fish-shrimps) but other important, feeding relationships (caterpillars-trees, salps-pico-plankton) fall far outside the 0.05–0.15 range usually assumed, with many ≫ 1.0.

Extending an earlier analysis (Longhurst 1990) a review of >100 pairs of prey and
Fig. 6. Size-structured compartment flux formulation based on discussions at a NATO Advanced Studies Institute in 1988. To the original has been added the flux of submicron particles from flagellate feeding (Koike et al. 1990) and also the role of marine viruses in lysing bacteria during algal blooms (Bratbak et al. 1990; Proctor and Fuhrman 1990).
predators (from picoplankton to whales) in the pelagic ecosystem, selected to cover all kinds of feeding mechanisms, gives the results shown in Fig. 7. Prey really are usually smaller than predators, but the linear ratio is 0.65 (±1.621) in these selected samples. The high variance suggests that we should place little reliance on the actual value of this ratio, and it is unlikely that increasing the data base would reduce the scatter. For metazoans, the ratio covers five orders of magnitude; high values (1.2–9.09) occur among protists, copepods, ctenophores, heteropods, fish, and cetacea, while the lowest values (0.0001–0.001) occur in fish, salps, and pteropods. Taxonomic position (except for protists) and relative abundance do not appear capable of predicting the ratio—even in the most approximate manner.

Such results suggest that strict linearity in biomass spectra must be to some extent an illusion. Because such models can have realistic output, we can only assume that there is internal balance between the consequences of shortcuts up the size-structured food chain and reverse flow back along it.

Response of the biological pump to forcing at different time scales

After this short excursion into our uncertainty about the mechanism of the biological pump and how to model it, we can return to the question of how the ocean, including its biota, may mitigate or reinforce the rate of increase of greenhouse gases in the atmosphere. More fashionably (e.g. Moore and Bolin 1986), this question is of-
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ten posed as "what part of the CO₂ emissions has the ocean already assimilated?" or "where is the missing CO₂ sink?" It is not surprising that answers are contradictory given the low accuracy and precision of our estimates of the relevant fluxes, although this problem often seems not to be recognized.

The quest for the missing CO₂ sink derives from our inability to balance present-day sources and sinks. Increases in the airborne fraction of CO₂ emissions and estimates of oceanic uptake fall short by about 1.2 Gt C yr⁻¹ of the canonical estimates of 6.3 Gt C yr⁻¹ emitted from all anthropogenic sources (Broecker et al. 1979; Detwiler and Hall 1988). The atmospheric increase is, of course, based on measurements with rather small error terms, but this is not the case for ocean uptake. Computation of flux into the ocean is based on box diffusion models, parameterized by uptake rates for passive tracers into the ocean (radon, tritium, bomb-¹⁴C), assumptions concerning ocean ventilation rates, transfer velocities of CO₂ across the surface, and rates of vertical mixing (e.g. Broecker et al. 1979; Oeschger et al. 1975); error estimates are usually not given for such models, which converge on oceanic uptake of 1.5-2.5 Gt C yr⁻¹. With median values, then, ~1.2 Gt C yr⁻¹ cannot be accounted for and represents the missing CO₂.

Balance could be obtained if the terrestrial biosphere was a net sink of C (Tans et al. 1990; Siegenthaler and Oeschger 1987). However, terrestrial ecologists concur that there is presently a net flux of CO₂ from the terrestrial biosphere to the atmosphere at a median rate of 3.25 Gt C yr⁻¹ (Woodwell et al. 1978; Houghton et al. 1987; Detwiler and Hall 1988). That this result is contrary to what is apparently required to balance global geochemical models is acknowledged (e.g. Houghton et al. 1987; Mellilo et al. 1990), although no convincing solution to this paradox has been advanced. These calculations accommodate soil weathering, forest clearance and regrowth, and growth stimulation by increasing atmospheric pCO₂, for which there is little direct evidence at present (Detwiler and Hall 1988; Kohlmaier et al. 1987).

Of the many estimates for flux terms that geochemical budgets require, most are of an accuracy that would cause them to be rejected by an experimental scientist. From Fig. 2 we could select values to support contradictory conclusions concerning the amount of imbalance (or even its existence) and the sink(s) to which the missing CO₂ must have gone. As it happens, Detwiler and Hall (1988) have already done this: using high values for oceanic uptake and low values for fossil fuel and forest clearance, they showed that it is possible to balance the budget within 0.3 Gt C yr⁻¹, which is a negligible quantity. If we reverse their argument and use high emissions and low ocean uptake, the missing CO₂ sink can become 2.3 Gt C yr⁻¹. Updating their argument and using the range of estimates now available for flux from the terrestrial biosphere (e.g. Houghton et al. 1987; Woodwell et al. 1978), we can obtain an excess of sources over sinks ranging from 0.2 to 13.1 Gt C yr⁻¹. In view of such great uncertainties, strong justification is needed to work with computations based on values chosen simply because they lie centrally in the scatter of estimates.

A recent study (Tans et al. 1990) illustrates this difficulty. A global data base of oceanic mixed-layer pCO₂ is used together with assumptions of transfer velocity of CO₂ across the sea surface to suggest that observed differences in atmospheric pCO₂ between the northern and southern hemispheres require a mid-northern latitude sink of 1.5-2.0 Gt C yr⁻¹ for which it is suggested that the terrestrial biosphere is the best candidate. No statistics are provided for the pCO₂ocean data base, but it is known that this is highly variable on the scale of days to weeks; in fact, because this variability is driven by growth of phytoplankton, pCO₂ is probably at least as patchy as the chlorophyll field seen in satellite imagery. Regional computations of pCO₂ in the mixed layer, therefore, can be no better than the notoriously unreliable regional estimates of chlorophyll or primary production based on ship data. Even supposing that the transfer velocity assumptions used in this study are correct, the level of uncertainty of the associated pCO₂ocean data base seems quite inadequate with which to challenge the can-
on of terrestrial ecology concerning the sign
of C flux with the atmosphere.

What are we to make of all this? Probably
we should admit that the fashionable ques-
tion (where has the apparently unaccount-
ed-for CO₂ gone to?) is not very profitable,
as are global geochemical models in which
interplay across the range of estimates for
each flux is not permitted. Unless the flux
from the terrestrial biosphere is really at the
very lowest end of all current estimates, we
should admit the possibility that our esti-
mate of ocean uptake may be far too low.
New thinking on this flux is appropriate.
Since most scenarios for change in pCO₂ atm
during glacial-interglacial transitions re-
quire some perturbation of the biological
processes of the photic zone, the first point
that we ought to explore is whether the bi-
ological pump is presently in steady state
(if, indeed, a steady state can be envisaged
given the lack of concordance of the time
scales relevant to the rotary, the archime-
dean, and the reciprocating pumps). And,
secondly, how do we expect it to be per-
turbed as climate changes induced by green-
house gases begin to manifest themselves?

The significance of these to points is easily
overlooked. Unless we overturn our basic
concept of phytoplankton limitation by in-
organic nutrients and accept some form of
C limitation, the biological pump cannot
respond to increasing pCO₂ in surface wa-
ters unless nutrient limitation in the photic
zone is relaxed. Only if we think that this
(or the opposite case) has already occurred,
because of changing global weather and cir-
culation patterns, could we claim that the
marine biosphere has already modified the
rate of increase of atmospheric CO₂.

Is the biological pump already per-
turbed?—Fisheries scientists need knowl-
edge of interannual variation in fish stocks,
so information on decadal-scale variability
in ocean circulation, and the distribution of
biota is available for many parts of the ocean.
It is certainly premature to conclude that
any of the trends seen in these data reflect
the effects of increased greenhouse gases,
but they do indicate how rapidly ocean bi-
ota can respond to changes in wind patterns
resembling those likely to occur as radiative
effects strengthen.

The most profound quasi-periodic event
in ocean circulation is El Niño/Southern
Oscillation (ENSO). During the 1982–1983
event, pCO₂ atm ceased to increase, only to
rebound immediately afterward to above the
accustomed 1.5 ppm yr⁻¹ (Volk 1989a;
Keeling and Revelle 1985). This global per-
turbation must have involved transfers be-
tween anomalous sources and sinks—
changes which interacted to produce the ob-
served signal in the atmosphere.

The reduced upwelling and deeper mixed
layer over the eastern tropical Pacific Ocean
during the 1982–1983 ENSO caused a re-
duction of primary production to 29% in
the equatorial upwelling, normally respon-
sible for 20–50% of global new production,
and a reduction to 10% of the normal area
of the Peru-Chile upwelling region (Barber
and Chavez 1986; Walsh 1988). Such a de-
crease in export flux might be expected to
result in increased outgassing of CO₂ at the
anomalously warm sea surface (Siegenthaler
1990). However, measurements (Feeley et
al. 1987) and simulations (Volk 1989a) sug-
gest that during 1982 the equatorial ocean
ceased to be a net source for CO₂ because
weaker upwelling reduced the near-surface
supply of CO₂-rich deeper water. Weaker
upwelling and reduced plant growth inter-
acted to determine transfer rates of CO₂
across the sea surface. Since the effect of
ENSO drought conditions reduces plant
growth in monsoon regions, the observed
changes in the atmospheric pCO₂ during
the 1982–1983 ENSO requires major intermit-
tent sinks during an ENSO event in higher
latitude oceans or in the nontropical terres-
trial biosphere.

Events on a longer time scale may also
have important effects on biological pro-
duction. Decadal increases in wind strength
and wave height in the northern hemisphere
may explain decadal increase in chlorophyll
values in the North Pacific gyre through in-
creased vertical transport of nutrients (Ven-
rick et al. 1987; Carter and Draper 1988).
Anomalous and sustained northerly winds
in the northeast Atlantic resulted in a de-
cadal-scale surface salinity anomaly that was
advected oceanwide in the thermohaline
circulation. This event has been invoked to
explain changes in the abundance and tim-
ing of diatom blooms and a reduction by half of high latitude primary production due to increased mixed-layer stability during its passage (Cushing 1990).

**Potential responses of the biological pump to an anthropogenic greenhouse climate**— Our predictions for the response of the marine biosphere to a changed climate can be no better than the available predictions for how ocean circulation will change with the climate. The main outlines, though not regional details, of changes in circulation have been predicted (Manabe and Stouffer 1980): weaker meridional thermal gradients will decrease polar ice cover, decrease the strength of the tradewinds and—at least during a period of transition—strengthen the flow of low-salinity surface water from the polar regions. In some situations, increased thermal gradients may develop between continental mass and adjacent ocean so that coastal upwelling may be enhanced (e.g. Bakun 1990). It is difficult to predict the balance of the various biological responses to these changes, which may be of opposite sign in low and high latitudes.

Can we get any help by reference to the response of the marine biosphere to changes in wind-stress patterns so as to mediate glacial transitions? Can we assume that after a period of rapid and perhaps chaotic response to the present anomalous rate of increase of atmospheric $p$CO$_2$, the biogeochemical balance will attain a quasi-steady state resembling the much slower rate of change at a glacial transition? Output from a two-dimensional model of Baes and Killoough (1986) appears to confirm, in fact, that biological uptake of C by the marine biosphere is capable of important modification of atmospheric CO$_2$ levels: an ocean with no biological uptake induces a doubling of atmospheric CO$_2$, and a doubling of nutrient supply to the phytoplankton almost halves atmospheric CO$_2$. Much smaller changes in atmospheric CO$_2$ are induced by halved or doubled circulation rates in the absence of biological processes.

There are also suggestions concerning other potential changes likely to occur if the anthropogenic greenhouse effect strengthens. Ice cover in the Arctic decreased ~5% between 1979 and 1987 (recalling the current global retreat of glaciers) and a further decrease of the magnitude suggested by climate scenarios is computed to increase levels of primary production over presently ice-covered Arctic shelf areas by an order of magnitude, or to about ~1 Gt C yr$^{-1}$ (Walsh 1989). This process, by sequestering C to the sediments, would reduce the rate of increase in atmospheric $p$CO$_2$ levels and may already have started to take effect, if observations of reduced Arctic ice cover in recent years are correct.

On the other hand, any oceanic primary production processes presently driven by wind stress at the sea surface and consequent renewal of photic zone nutrients (equatorial upwelling, event-scale mixing, and perhaps spring blooms driven by winter overturn) will become weaker and reduce the present rate of C sequestration: the so-called phytoplankton accelerator effect in relation to increasing $p$CO$_2$atm. However, as noted above, there is evidence that in recent decades, when the first effects of increased greenhouse gases may be expected to have taken effect, these processes may have become stronger rather than weaker in midhigh latitudes of the northern hemisphere.

**Conclusions**

Several conclusions can now be drawn concerning our original question: will the marine biosphere mitigate or reinforce the rate of increase of anthropogenic $p$CO$_2$atm?

Our first conclusion must be that the output from formal biogeochemical models deployed for this purpose should be accorded less deference than has become customary, given our extreme uncertainty about the rates of almost all critical fluxes and even of the size of the stocks between which flux occurs. Where such models do not accommodate reasonable error terms for each flux and stock, their output should be regarded with great caution.

The second conclusion concerns the paradox that highly aggregated simulation models of biochemical processes in the pelagic should give output within observational constraints, although their formulation departs so strikingly from our emerging understanding of flow within protistan food
webs. Perhaps the complexity of simulated processes is, in reality, lost as noise in the overall signal representing the fluxes simulated, or perhaps, since we know approximately what constraints to place on outputs, we may unconsciously parameterize the models accordingly. Output may be correct, but if network flow is incorrect, predicted responses to novel conditions may be fallacious. Thus, a way must be found to subsume the dispersion of function in procaryotes and eucaryotes (still very largely undescribed, but becoming more complex with each new finding) into a few interacting compartments, representing dispersed functions rather than groups of taxa, as is the current practice.

If we do not defer to geochemical models to answer our question, can we obtain any help from scenarios of the role of biota in \( p\text{CO}_2\text{atm} \) changes during glacial transitions? Can these scenarios be a guide to biotic response to other global perturbations? If this is so, and if the changed greenhouse climate is to be dominated by a reduced meridional thermal gradient (reduced meridional wind stress), then we can at least guess what the sign of the biotic response will be. It is more likely that \( C \) uptake by the marine biosphere will weaken rather than strengthen and consequently will enhance the rate of increase of \( p\text{CO}_2\text{atm} \) rather than mitigating the effect. Hopefully, in the foreseeable future, it will be possible to upgrade this guess (through the step of being a plausible scenario) to a predictive model on which we can place some confidence.

References


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