

A sensitivity study of the effect of global change on ocean carbon uptake

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ABSTRACT

A two-dimensional global model of ocean chemistry and biology is used to calculate the sensitivity of oceanic CO₂ uptake during the next century to various biological and chemical feedback mechanisms. Model formulations are outlined and the model is validated for current conditions by comparison with data on ¹⁴C and bomb-¹⁴C, primary production, nitrogen, oxygen and DOC. The model includes several mechanisms that are influenced by global change: temperature effects, circulation rate, calcification, UV-damage, eutrophication and CO₂ fertilization. It is concluded that a temperature increase could provide a substantial positive feedback by its effect on ocean chemistry, decreasing carbon uptake by 16%. Biological mechanisms modify oceanic uptake to a relatively minor extent (some 5%) only, implying that abiotic models of anthropogenic CO₂ uptake are expected to give essentially the same answers as models including a biological carbon cycle.

1. Introduction

Models of the oceanic uptake of anthropogenic CO₂ (Maier-Reimer and Hasselmann, 1987; Sarmiento et al., 1992) have generally focused on ocean physics and chemistry, leaving out the biological carbon cycle. Although the biological “pumps” obviously influence CO₂ storage, this may not be relevant in a study of the current anthropogenic perturbation of the carbon cycle, as long as the biological cycle would not be modified by global change. However, paleoclimatological models have indicated that even relatively minor changes in the biological cycle may affect oceanic CO₂ storage (Dymond and Lyle, 1985; Boyle, 1988; Sarmiento et al., 1988; Mix, 1989).

Although there are similarities between the glacial-interglacial transitions and the currently predicted changes in climate, there are also clear differences, of which the most important is the much shorter time scale of the current change. Previous studies addressing the effect of global

change on ocean biology and chemistry have indicated very limited effects only. However, these studies generally had a rather limited scope: Fogg (1991) considered only changes in productivity over a 30-year period while Peterson and Melillo (1985) considered eutrophication effects only. The separate treatment of individual effects of global change is not easily integrated into an overall impact. The cycles of nutrients, alkalinity and carbon are closely linked and provide numerous feedbacks, requiring some quantitative model of their net effect.

Such a model is provided by Maier-Reimer (1993) and shows a negligible difference between anthropogenic carbon uptake by an abiotic model and one including a biological pump. However, his model treats phosphorus rather than nitrogen as the limiting nutrient. This choice can be motivated on a geological time scale (Broecker and Peng, 1982), but for the present-day ocean N rather than P limits productivity (Fogg, 1991). Although N and P are closely correlated (making the overall picture of productivity of an N- or P-based model very similar), the residence time of P is approximately 40 times longer, which makes a large

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difference in an assessment of eutrophication effects. Another factor of potential importance not taken into account by Maier-Reimer (1993) is the dissolved organic carbon (DOC). Because of its size (700–2000 GtC, Toggweiler, 1992), a change in the DOC pool could be an important factor in the global carbon budget. A preliminary study (Klepper et al., 1994) indicated that an increase in the decay of DOC (either because of temperature effects or from increasing UV radiation) could be an important feedback mechanism.

In this study we use a model of biology and chemistry to investigate possible feedbacks from CO₂-induced global change on the oceanic carbon cycle. The biological model is nitrogen based, and includes the cycles of alkalinity (Ca), DOC and oxygen. The biological and chemical model is coupled to a 2-dimensional transport field. A standard run of the model (including only the direct feedback from pCO₂ on carbonate chemistry) is compared to a number of runs including various feedback mechanisms. The effect of these mechanisms is evaluated by calculating carbon uptake during the next century.

2. Methods

2.1. Model formulation

Ocean circulation is described on a 2-dimensional (latitude × depth) grid with an Atlantic and an Indo-Pacific branch, linked below 40°S in a single Antarctic ocean. Resolution is 10° latitude and 400 m depth (maximum depth 4000 m), with the surface layer split in a well-mixed layer of variable depth (40–200 m) and a transition layer making up the difference to 400 m. Advective flows are based on tracer distributions as reviewed by Keir (1988), see Fig. 1. Horizontal mixing is set at $6 \cdot 10^3 \text{ m}^2 \text{ s}^{-1}$ in the surface layer and $7.1 \cdot 10^2 \text{ m}^2 \text{ s}^{-1}$ in deeper layers; vertical mixing at $1.2 \cdot 10^{-3} \text{ m}^2 \text{ s}^{-1}$ in polar oceans (> 60° latitude) and $6.5 \cdot 10^{-5} \text{ m}^2 \text{ s}^{-1}$ elsewhere.

Chemical equilibrium constants have been adopted from Gieskes (1974). Piston velocity was modelled as a function of temperature (T) as $V(T) = V(0)e^{0.026T}$. A quadratic relation with wind speed (approximating the curve of Liss and Merlivat, 1985) was tried but did not give realistic surface ¹⁴C distributions as a result of a large difference in piston velocity between the tropics and

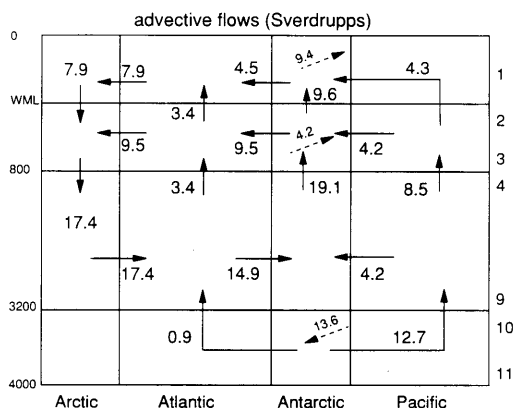


Fig. 1. Advective flows ($10^6 \text{ m}^3 \text{ s}^{-1}$). Dotted arrows indicate flows between southern circumpolar and Antarctic oceans.

high latitudes. This confirms results by Broecker et al. (1985) who concluded that tropical exchange rates differ from high-latitude rates only to a minor extent. For this reason a value of $V(0)$ independent of latitude was used. Its global averaged value (within a range of 3.5–6.0 m day^{-1} , Liss, 1984) was determined by calibration to bomb-¹⁴C data. Chemical equilibria and exchange rates were calculated for 2-month periods to obtain a yearly flux.

The biological model is based on the work of Klepper (1995) who showed that the yearly averaged output of a dynamical model (obtained by integrating the equations $\partial C/\partial t$) is practically identical to that of a quasi steady state model (obtained by solving the equations $\partial C/\partial t = 0$ for each time step). The quasi-steady state approach speeds up calculations and permits model reduction: in steady state, predator to prey ratios are constant, making it possible to represent grazing by a single phytoplankton mortality rate. It can be shown (Klepper, 1995) that a 7-compartment oceanic foodweb model (resembling models reviewed by Steele and Henderson, 1992) is (from a yearly averaged perspective) equivalent to a much simpler 3-compartment model, containing only inorganic nutrients, phytoplankton and a single heterotrophic compartment. The main aim of this simple biological model is to use the steady state values of the “fast” fractions in the biological model to calculate the transfer rates between the “slow” variables (total N, total C, Ca): the transfer of particulate matter to deeper layers and to DOM

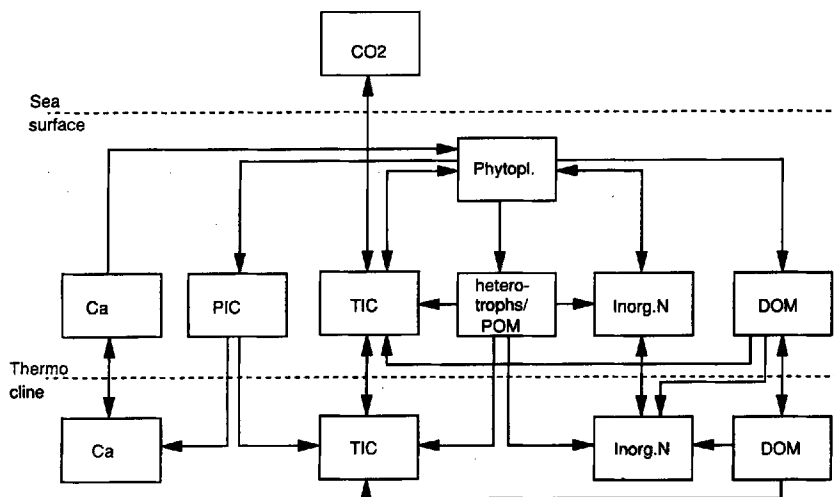


Fig. 2. Compartment diagram of organic and inorganic pools of C, N and Ca showing linkages between ocean-atmosphere exchange, transport (double-headed arrows) and biological transformations.

(as excretion). The linkage between various pools in the model is shown in Fig. 2.

The phytoplankton balance equation reads:

$$\frac{dB}{dt} = B \left(P_{\max} f(I) \frac{N}{N + k_N} \times \frac{CO_2}{CO_2 + k_{CO_2}} - r - m - e \right) g(T),$$

with:

- B : phytoplankton biomass (mole kg^{-1})
- N : inorganic nitrogen (nitrate + ammonium; mole kg^{-1})
- $P_{\max}$: maximum production rate (day^{-1})
- $f(I)$: light-limitation function (-)
- k_N : half-saturation for nitrogen (mole kg^{-1})
- k_{CO_2} : half-saturation for CO_2 (mole kg^{-1})
- m : mortality (grazing) rate (day^{-1})
- r : respiration rate (day^{-1})
- e : DOC excretion rate (day^{-1})
- $g(T)$: temperature function (-), as:

$$g(T) = Q 10^{T/10}$$

$Q 10$: the relative increase in process rate for a 10° increase in T ;

for the heterotrophic compartment we have:

$$\frac{dD}{dt} = g(T) mB - \left(s g(T) + \frac{v}{z} \right) D,$$

with:

- D : biomass of heterotrophs, including detritus (mole kg^{-1})
- s : metabolic rate (day^{-1})
- v : sinking rate (m day^{-1})
- z : well-mixed layer depth (m)
- $g(T)$: as above (-).

According to these equations, the light and temperature conditions determine steady state nutrient concentration. The steady-state between the three "fast" N fractions (inorganic N, phytoplankton and heterotrophs, but excluding the more refractory dissolved organic matter) determines an export flux of particulate matter. In combination with the transport model, this export flux determines the "slow" change in total N and C. These calculations resemble those for inorganic carbon, where the "slow" change in TIC due to atmospheric exchange is determined by the equilibrium distribution of H_2CO_3 , HCO_3^- and CO_3^{2-} . The biological equilibrium states are calculated for 2-month periods to obtain a yearly flux.

The DOM is split into a refractory and a very refractory pool; labile DOM is not modelled, as

being of little geochemical significance (its excretion and immediate heterotrophic utilization can be considered to be included as respiration). For the "slow" variables we do not assume steady state but calculate time-dependent solutions (which only reach steady state after centuries or more).

The cycles of other elements in the model (C, ^{14}C , O, Ca) are connected with the nitrogen cycle. This implies 3 carbon pools (inorganic and two DOC pools) and 3 associated ^{14}C pools. For oxygen, we assume surface equilibrium. Calcium is removed (as CaCO_3) from the surface proportionally to gross primary production: in contrast to nitrogen, it is assumed that loss processes (respiration, grazing) do not lead to a release of dissolved calcium. Of the settling Ca-flux, 17% is permanently removed (Wollast, 1981), the rest is assumed to dissolve in the deepest layer (3600–4000 m). Alkalinity is calculated from Ca and N-distributions.

Input rates of N, C (as DOC and DIC) and Ca were adopted from Wollast (1981). Parameter values for the biological model were adjusted (within the range of literature values as reviewed by Parsons et al., 1984) to agree with observed primary production, nutrient and DOC values.

2.2. Feedback mechanisms

Under this heading we have included not only possible direct effects of CO_2 increase, but also indirect effects and processes closely correlated to CO_2 increase.

CO_2 increase may stimulate phytoplankton production (Riebesell et al., 1993). This has been included by changing the half-saturation value in the CO_2 limitation function in the phytoplankton growth equation from 0 to $10\ \mu\text{M}$, while increasing P_{max} in order to obtain the same productivity for present-day CO_2 levels. The possible effect of increasing $p\text{CO}_2$ on calcification is unclear, but a decrease seems most likely. Calcification is apparently a mechanism to aid carbon uptake at low $p\text{CO}_2$ (Dong et al., 1993) and the supersaturation of seawater relative to CaCO_3 probably facilitates the process (Lewin, 1962). Some 10–50% of the CaCO_3 formed is in the form of aragonite (Berner and Honjo, 1981), which dissolves at shallow depths. Both the increase in $p\text{CO}_2$ and the associated decrease in CaCO_3 saturation would tend to decrease net calcification.

This has been modelled by making calcification proportional to CaCO_3 saturation.

Temperature increase is projected to vary between 1.5 and 4.5°C for air surface temperature (Houghton et al., 1992). Some models predict that sea surface temperatures (SST) will follow this increase by 70–80% (Stouffer et al., 1989), while others (De Haan et al., 1994) calculate an increase in SST that is approximately 50% of surface air temperature. In the present study we have investigated the effect of a global average SST increase of 4°C by 2100, latitudinally distributed as predicted by De Haan et al. (1994). This will affect both abiotic CO_2 uptake (chemical equilibrium conditions and exchange rate) and the biological cycle (increased process rates). The two temperature effects have been included separately.

UV radiation will increase due to stratospheric ozone depletion. This may decrease biological productivity by some 9% (Smith et al., 1992). UV has been assumed to affect light- and nutrient saturated productivity only, but not the light limited rate nor nutrient affinity. Another UV-related feedback may be by an increased destruction of DOC. This has been included by assuming the most refractory DOC fraction to be decomposed by UV with an action spectrum equal to the absorption spectrum of DOC (Moffet, 1990). These assumptions lead to a 6% increase in effective dose due to halving of the ozone concentration.

The effect of *eutrophication* has been studied by assuming riverine input of inorganic N to double during the next century.

Ocean circulation is projected to decrease as a result of climatic change (Mikolajewicz et al., 1990), affecting both physical-chemical uptake of CO_2 and the biological cycle (nutrient supply). In the simulations of Mikolajewicz et al. the North Atlantic deep water formation gradually decreases to one third of its original volume in the year-50 of the simulation period, the Southern Ocean deep water formation decreases by a one third of its volume in 35 years but afterwards recovers half of this loss. In our calculations the deep water formation is assumed to change in the period 1990 to 2040 and to remain constant afterwards.

The standard run of the model does not include feedbacks apart from the shift in carbonate equilibrium due to increased $p\text{CO}_2$. The effect of feedbacks has been studied by calculating the

cumulative uptake by the ocean with a prescribed atmospheric concentration (reaching 785 ppmv in 2100). The time-course of the change in circulation is described above, changes in temperature, UV radiation and nitrogen input have been assumed to follow a function $p(t) = p_0 + (p_\infty - p_0)(1 - e^{-t/c})$ with t starting in 1990 and c a value of 40 years (Mikolajewicz et al., 1990).

3. Results

3.1. Steady state and current climate

Model output (which gives latitudinally averaged results) and latitudinally averaged measurements from the GEOSECS program (Takahashi et al., 1981) have been plotted as latitude-depth graphs. This allows both a comparison of absolute values

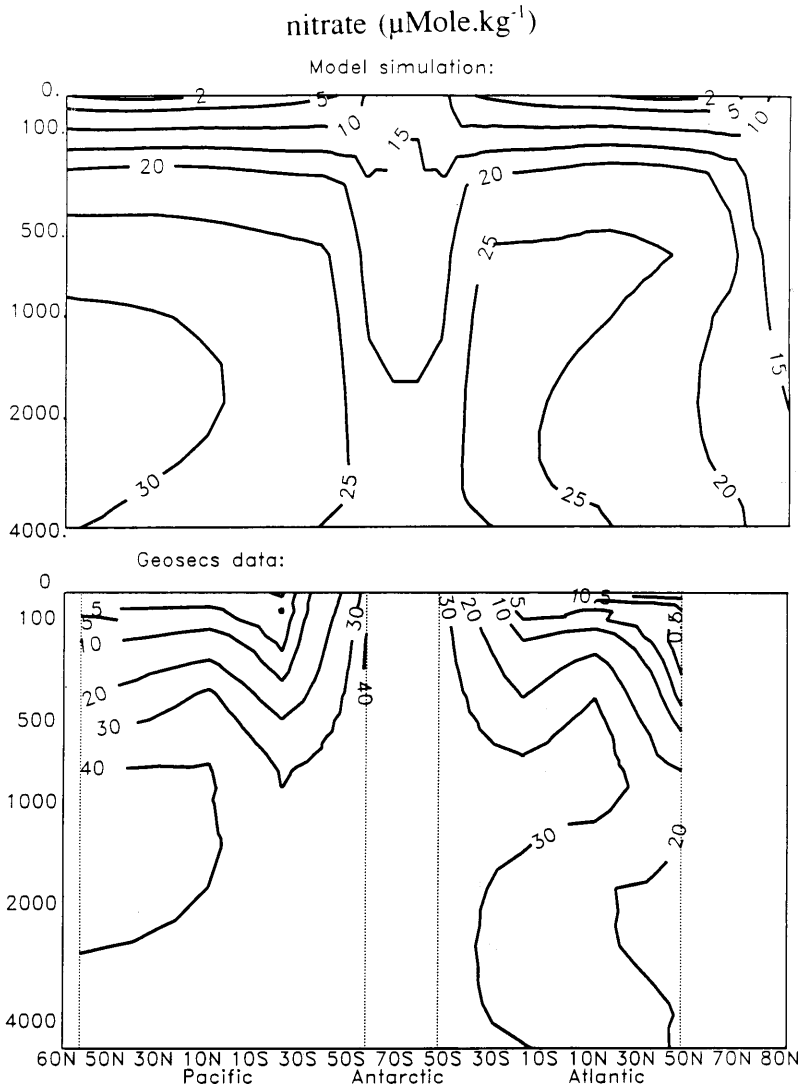


Fig. 3. Nitrate concentrations: model and observations (Takahashi et al., 1981).

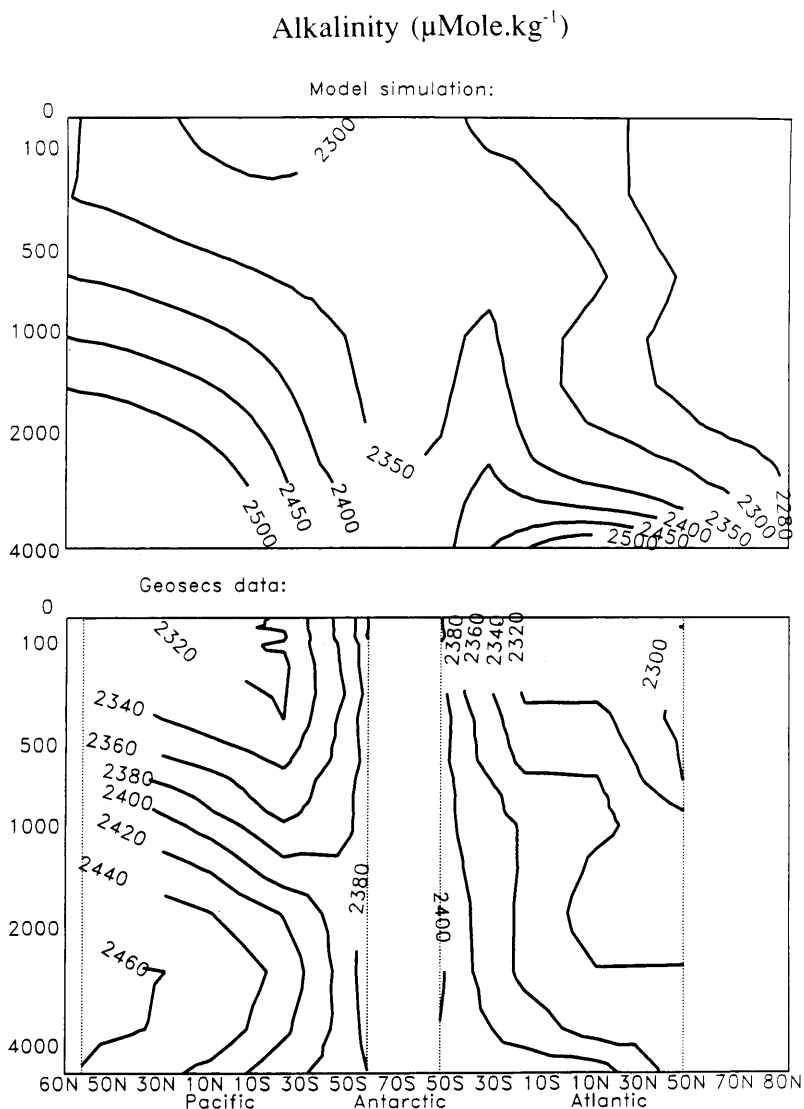


Fig. 4. Alkalinity: model and observations (Takahashi et al., 1981).

at a certain depth/latitude and a comparison of general patterns (gradients, location of minimum, etc.). The results generally show good agreement with measurements. Steady state results for nitrogen (Fig. 3) alkalinity (Fig. 4) and ^{14}C (Fig. 5) closely agree with GEOSECS data; similar agreement was found for oxygen and total carbon. Simulated values for DOC (Fig. 6) agree with recent HTC estimates of $80\text{--}100 \mu\text{Mole kg}^{-1}$

at depth to $200\text{--}250 \mu\text{Mole kg}^{-1}$ at the surface (Toggweiler, 1988), and with radiocarbon activities (Bauer et al., 1992) between -550‰ in the deep Pacific and -400‰ in the deep Atlantic to -200‰ at the surface. The geographical distribution of primary production does not agree well with measurements (Fig. 7), but its average value ($72 \text{ gC m}^{-2} \text{ y}^{-1}$) is close to the estimated averages of $60 \text{ gC m}^{-2} \text{ y}^{-1}$ (Berger, 1989) and

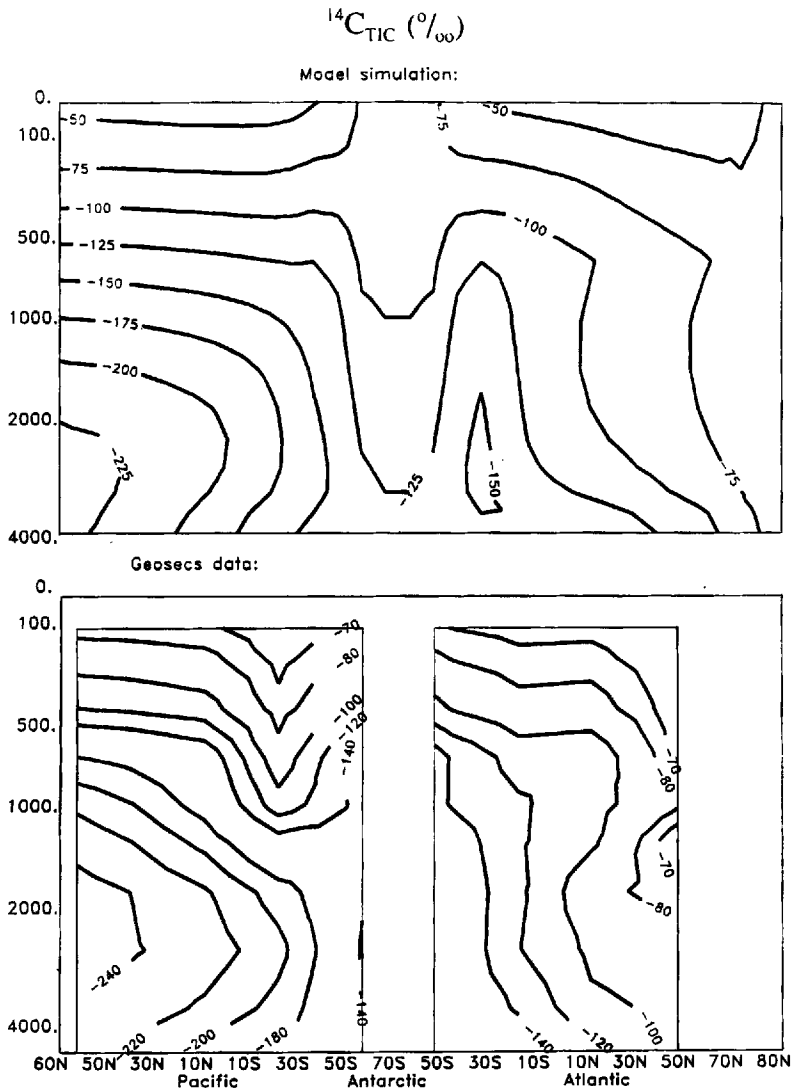


Fig. 5. Radiocarbon (in ‰ relative to atmospheric equilibrium): model and observations (Stuiver et al., 1981).

$86 \text{ gC m}^{-2} \text{ y}^{-1}$ (Platt and Subba Rao, 1975). Average new production is calculated as $12.6 \text{ gC m}^{-2} \text{ y}^{-1}$ in the range of $9.6\text{--}13.2 \text{ gC m}^{-2} \text{ y}^{-1}$ estimated by Eppley and Peterson (1979).

After reaching steady state at an atmospheric pCO_2 of 280 ppmv the model was forced with observed atmospheric concentrations of CO_2 and ^{14}C . The calculated ΔpCO_2 (Fig. 8) in 1987 is in good agreement with observations (Tans et al.,

1990). Uptake of bomb- ^{14}C in 1974 was constrained to match the GEOSECS value of $8.3 \cdot 10^9$ atoms cm^{-2} (Broecker et al., 1985) by adjusting piston velocity. This required a piston velocity of 5.7 m day^{-1} , 18% higher than the GEOSECS estimate of 4.8 m s^{-1} (Liss, 1984). Average penetration depth was calculated as 300 m, 14% below the GEOSECS average of 350 m (Broecker et al., 1985). Atmospheric uptake of anthropogenic CO_2

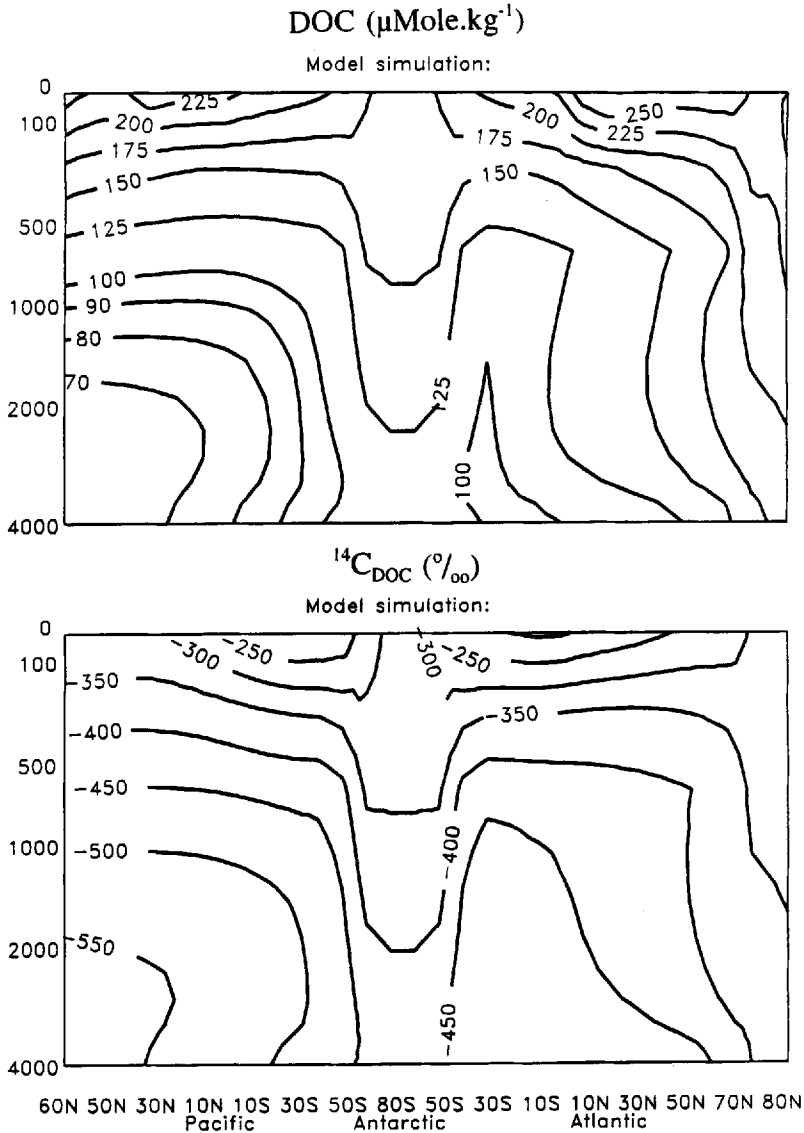


Fig. 6. Dissolved organic carbon: model results for concentrations and DO^{14}C .

(i.e., correcting for pre-industrial efflux) during 1980–1989 is 1.37 GtC y^{-1} , within the IPCC range of $2.0 \pm 0.8 \text{ GtC y}^{-1}$ (Houghton et al., 1990).

3.2. Feedback mechanisms

When the model was forced with increasing pCO_2 , the standard version of the model has stored a total of 394 Gt anthropogenic carbon in

the ocean in the year 2100. The modifications of this amount by various feedback mechanisms are shown in Table 1. It can be observed that the most important positive feedbacks are related to temperature and its effect on chemistry, biology and DOC decomposition. Together, this may cause a decrease in storage of 100 Gt. Negative feedbacks are provided mainly by a decreased calcification

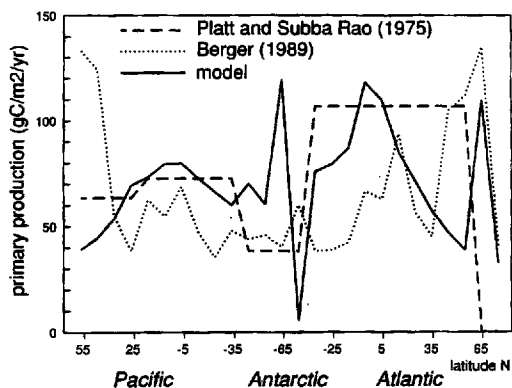


Fig. 7. Primary production: model and observations.

(40 GtC), CO_2 fertilization (17 GtC) and eutrophication (7 GtC); in combination, these could lead to an extra storage of 71 GtC.

4. Discussion

The present model has some obvious flaws, in particular in the description of the transport field. The model does not reproduce some of the spatial structure apparent in the data, in particular the use of a single upwelling rate for both tropics and temperate zones of each ocean basin is not realistic. In addition, the hydrodynamic transport (affecting the penetration depth of bomb- ^{14}C) is apparently underestimated, requiring a rather high value of air-sea transport rate. However, for a global

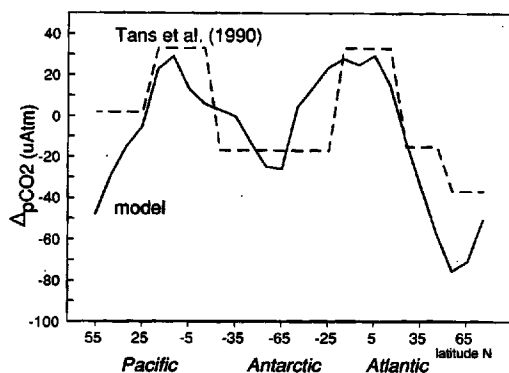


Fig. 8. 1987 surface ocean ΔpCO_2 : model and observations.

Table 1. Effect of various feedback mechanisms on storage of anthropogenic carbon in 2100

Feedback mechanism	Likelihood	ΔS (GtC)
temperature effects on chemistry	+	-62
temperature effects on biology	+	-16
temperature effects on DOC decay	+	-5
CO_2 fertilization	-	+17
decreased calcification	-	+40
increased UV: stimulation of DOC decay	-	-2
increased UV: decrease in productivity	o	-5
eutrophication	-	+7
decreased circulation	o	-16
all positive feedbacks combined	-	-100
all negative feedbacks combined	--	71

Basic storage (S) is 395 GtC, effects are expressed as ΔS . The column "likelihood" indicates authors' subjective estimate ranging from unlikely (-) to probable (+).

averaged value of carbon fluxes spatial details may not be very important. Furthermore, for the present sensitivity study our main interest is in the biological cycle rather than in the physical-chemical pump. The fact that global averages of both total and "new" primary production and the concentrations of substances most sensitive to the biological cycle (nitrogen, oxygen, DOC) are well reproduced appears to make the present model a valid basis for an estimate of the relative magnitude of feedback effects.

In the assessment of possible global-change induced mechanisms one must necessarily be speculative ("what if the presently observed change near Antarctica would be extrapolated to the entire ocean?") without making completely unrealistic assumptions ("without the biological carbon pump, atmospheric pCO_2 would double"). The estimated effects of feedback mechanisms in Table 1 are therefore intended as upper bounds to speculations rather than actual predictions. For example, it is unlikely that *all* phytoplankton would respond to increased pCO_2 or that *all* riverine N-inputs would double. Our estimate of the likelihood of particular changes has been entered in Table 1. As can be noted, positive feedbacks (leading to a decreased storage) seem more likely than negative ones. Adding all positive feedbacks would decrease storage by 100 GtC (-25%), adding all negative feedbacks gives an extra storage of 71 GtC (+18%).

Obviously, neither of these extremes is likely to occur. Due to large uncertainties an overall assessment is difficult, but the most likely result appears to be a net positive feedback in the order of 20% of oceanic uptake. It appears that the most important feedback results from temperature effects on

chemistry; possible changes in calcification rates could be important but are highly speculative. It seems that these results confirm the conventional approach to focus on physical and chemical models in the calculation of anthropogenic carbon uptake.

REFERENCES

- Bauer, J. E., Williams, P. M. and Druffel, E. R. M. 1992. ^{14}C activity of dissolved organic carbon in the north-central Pacific and Sargasso Sea. *Nature* **357**, 667–670.
- Berger, W. H. 1989. Appendix: global maps of ocean productivity. *Productivity of the oceans: present and past*. John Wiley. 429–455.
- Berner, R. A. and Honjo, S. 1981. Pelagic sedimentation of aragonite: its geochemical significance. *Science* **211**, 940–942.
- Boyle, E. A. 1988. The role of vertical chemical fractionation in controlling later quaternary atmospheric carbon dioxide. *J. Geophys. Res.* **93**(C2), 15701–15714.
- Broecker, W. S. and Peng, T. H. 1982. *Tracers in the sea*. Palisades, N.Y., Eldigio Press, Columbia Univ.
- Broecker, W. S., Peng, T. H., Ostlund, G. and Stuiver, M. 1985. The distribution of bomb radiocarbon in the ocean. *J. Geophys. Res.* **90**(C4), 6953–6970.
- Dong, L. F., Nimer, N. A., Okus, E. and Merret, M. J. 1993. Dissolved inorganic carbon utilization in relation to calcite production in *Emiliana huxleyi* (Lohmann) Kamptner. *New Phytol.* **123**, 679–684.
- Dymond, J. and Lyle, M. 1985. Flux comparisons between sediments and sediment traps in the eastern tropical Pacific: Implications for atmospheric CO_2 variations during the Pleistocene. *Limnol. Oceanogr.* **30**, 699–712.
- Eppley, R. W. and Peterson, B. J. 1979. Particulate organic matter flux and new production in the deep ocean. *Nature* **282**, 677–680.
- Fogg, G. E. 1991. Changing productivity of the oceans in response to a changing climate. *Annals of Botany* **67**, 57–60.
- Gieskes, J. M. 1974. The carbonate chemistry of the ocean. *The sea*. Wiley & Sons, pp. 125–131.
- Haan, B. J. de, Klepper, O., Krabec, J., Krol, M. S. and Olendrzynski, K. 1994. An atmosphere-ocean model for integrated assessment of global change. *Water, Air and Soil Pollution* **76**, 283–318.
- Houghton, J. T., Jenkins, G. J. and Ephraums, J. J. 1990. *Climate change, the IPCC scientific assessment*. New York, Cambridge University Press.
- Houghton, J. T., Callendar, B. A. and Varney, S. K. 1992. *Climate change 1992. The supplementary report to the IPCC scientific assessment*. New York, Cambridge University Press.
- Keir, R. S. 1988. On the late Pleistocene ocean geochemistry and circulation. *Paleoceanography* **3**, 413–445.
- Klepper, O. 1995. Modelling the oceanic food web using a quasi steady state approach. *Ecol. Modelling* **77**, 33–41.
- Klepper, O., De Haan, B. J. and Van Huet, H. 1994. Biochemical feedbacks in the oceanic carbon cycle. *Ecol. Modelling* **75/76**, 459–469.
- Lewin, J. C. 1962. Calcification. *Physiology and biochemistry of algae*. New York, Academic Press. 457–465.
- Liss, P. and Merlivat, L. 1985. Air-sea gas exchange rates, introduction and synthesis. *The rôle of air-sea exchange in geochemical cycling*. Hingham, Mass., D. Reidel.
- Liss, P. C. 1984. Gas transfer: experiments and geochemical implications. *Air-Sea exchange of gasses and particles*. NATO ASI Series. 241–298.
- Maier-Reimer, E. 1993. The biological pump in the fossil fuel CO_2 uptake by the ocean. *Global Planet. Change* **8**, 13–15.
- Maier-Reimer, E. and Hasselmann, K. 1987. Transport and storage of CO_2 in the ocean, an inorganic ocean-circulation carbon cycle model. *Clim. Dyn.* **2**, 63–90.
- Mikolajewicz, U., Santer, B. D. and Maier-Reimer, E. 1990. Ocean response to greenhouse warming. *Nature* **345**, 589–593.
- Mix, A. C. 1989. Influence of productivity variations on long-term atmospheric CO_2 . *Nature* **337**, 541–544.
- Moffet, J. W. 1990. UV effects on homogeneous chemical processes. *Effects of solar ultraviolet radiation on biogeochemical dynamics in aquatic environments*. Woods Hole, Woods Hole Oceanog. Inst. Tech. Rept. 10–11.
- Parsons, T. R., Takahashi, M. and Hargrave, B. 1984. *Biological oceanographic processes*. Oxford, Pergamon Press.
- Peterson, B. J. and Melillo, J. M. 1985. The potential storage of carbon caused by eutrophication of the biosphere. *Tellus* **37B**, 117–127.
- Platt, T. and Subba Rao, D. V. 1975. Primary production of marine microphytes. *Int. Biological Programme* **3**, 249–279.
- Riebesell, U., Wolf-Gladrow, D. A. and Smetacek, V. 1993. Carbon dioxide limitation of marine phytoplankton growth rates. *Nature* **361**, 249–251.
- Sarmiento, J. L., Orr, J. C. and Siegenthaler, U. 1992. A perturbation simulation of CO_2 uptake in an ocean general circulation model. *J. Geophys. Res.* **97**(C3), 3621–3645.

- Sarmiento, J. L., Toggweiler, J. R. and Najjar, R. 1988. Ocean carbon-cycle dynamics and atmospheric $p\text{CO}_2$. *Phil. Trans. R. Soc. Lond.* **A325**, 3–21.
- Smith, R. C., Prezelin, B. B., Baker, K. S., Bidigare, R. R., Boucher, N. P., et al. 1992. Ozone depletion: ultraviolet radiation and phytoplankton biology in Antarctic waters. *Science* **255**, 952–959.
- Steele, J. H. and Henderson, E. W. 1992. The role of predation in plankton models. *J. Plankton Research* **14**, 157–172.
- Stuiver, M., Ostlund, H. G. and McConnaughey, T. A. 1981. GEOSECS Atlantic and Pacific ^{14}C distribution. *Carbon cycle modelling*. Chichester, Wiley & Sons. 201–221.
- Takahashi, T., Broecker, W. S. and Bainbridge, A. E. 1981. Supplement to the alkalinity and total carbon dioxide concentration in the world oceans. *Carbon cycle modelling*. Chichester, John Wiley and Sons. 159–199.
- Tans, P. P., Fung, I. Y. and Takahashi, T. 1990. Observational constraints on the global atmospheric CO_2 budget. *Science* **247**, 1431–1438.
- Toggweiler, J. R. 1988. Deep-sea carbon, a burning issue. *Nature* **344**, 468.
- Toggweiler, J. R. 1992. Catalytic conversions. *Nature* **356**, 665–666.
- Wollast, R. 1981. Interactions between major biochemical cycles in marine ecosystems. *Some perspectives of major biochemical cycles*. Chichester, Wiley & Sons, pp. 125–142.