

# CONSEQUENCES OF GLOBAL CHANGE FOR OCEANS: A REVIEW

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**Abstract.** The possible effects of global climate change on the oceans are described through a review of the results produced by GCM's that explicitly incorporate the dynamics of the interior of world oceans. Changes at asymptotic equilibrium influence the whole water column, but equilibrium in the deep sea is reached after several thousands years. The transient response of these models after 25 years following the onset of the perturbation (doubling or quadrupling of atmospheric CO<sub>2</sub>) affects the upper layer of the oceans (<1000 m) producing an increase in temperature between 2–4 °C. Models with realistic geography, as compared with simplified ones with N-S symmetry, produce warming near the north pole but a small cooling close to the antarctic continent. The main impacts of the predicted changes upon marine ecosystems are identified within several possible scenarios. Special mention is made of the expansion/contraction of pelagic habitats, oceanic island habitats, ocean wide distributional changes and the dynamical effects upon bioproduction.

## 1. Introduction

The purpose of this paper is to describe the possible effects on the oceans induced by global climatic change, with particular emphasis on the southern hemisphere. Accordingly, in the first place the evidence for global climatic changes is briefly summarized. Second, searching for some plausible oceanic scenarios derived from global climatic change, a partial review of current literature, on physics models of the coupled ocean-atmosphere system is presented. Third, and finally, the identification of main impacts of these changes on marine ecosystems is attempted.

Global climatic changes are expected from the increase in the CO<sub>2</sub> content of the atmosphere, mostly as the result of the burning of fossil fuels. Because CO<sub>2</sub> and other greenhouse gases exert differential absorption of radiating energy at different wavelengths, a net increase of global temperature is expected, caused by the shift in the global radiation budget between incoming and outgoing (mostly IR) radiation. Although CO<sub>2</sub> concentration in the atmosphere has changed dramatically in the past 40 000 years, with a distinct minimum at 20 000 years BP (Neftel *et al.*, 1982), and shows significant variability on the scale of centuries (Figure 1; Webster, 1985), direct instrumental measurements show at present a clear monotonic trend of increasing CO<sub>2</sub> (see the review by G. Pearman in this volume). Atmospheric CO<sub>2</sub> has increased from 280 to 300 parts per million in 1880 to 335 to 340 in 1980 (Hansen *et al.*, 1981), a trend that has already exceeded the between-centuries range of variation.

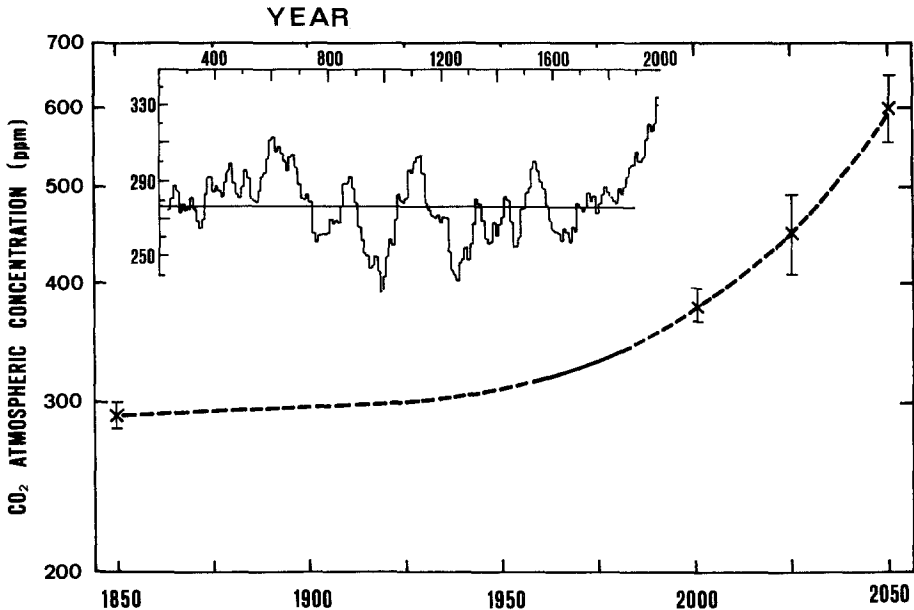


Fig. 1. Concentration of atmospheric CO<sub>2</sub> between 1850 and 2050. Actual record between 1958 and 1985, the rest of the curve is estimated. In the upper left, the variation of CO<sub>2</sub> between A.D. 200 and the present, as determined from <sup>13</sup>C content of tree rings, is shown. (Redrawn from Webster, 1985.)

If the earth is today experiencing CO<sub>2</sub> induced warming, its signature would be undetectable and confounded with 'climatic noise' in the instrumental record, since its magnitude would still be within the range of the natural variability of climate (Jones *et al.*, 1982). The predicted increase in temperature, based on conservative estimates of atmospheric CO<sub>2</sub> increase, indicates that the earliest confirmation of the warming trend could be observed in the instrumental record around year 1995 for an increase of 5.6 °C and around year 2000 for an increase of 1.4 °C (Hansen *et al.*, 1981; see also B. Pittock, this volume).

## 2. Modelling the Ocean Response to Increased CO<sub>2</sub>

Basic principles force the inclusion of oceanic compartments in coupled ocean-atmosphere models or General Circulation Models (GCMs); however, it is fair to say that modelling of the oceanic component in GCMs lags several years behind what has been achieved for the atmosphere. Therefore, it is important to distinguish models in which oceans are included in order to enhance the realism of global climate response of the atmosphere, from models in which the main goal is to fully predict oceanic changes themselves and their impact on global climate. However, major gaps exist in our knowledge of some oceanic processes, and therefore their parameterization is uncertain in the absence of new information. Of these

TABLE I: Characteristic times, in years, to reach equilibrium in the ocean-atmosphere model (from: Spelman and Manabe, 1984)

| Compartment           | Normal CO <sub>2</sub> | 4 × CO <sub>2</sub> |
|-----------------------|------------------------|---------------------|
| Atmosphere            | 7.8                    | 11.8                |
| Upper ocean (<1000 m) | 850                    | 1290                |
| Deep ocean (>1000 m)  | 23000                  | 35000               |

uncertainties, the various types of mixing in the oceans are the most crucial, particularly cross isopycnal mixing (Stewart and Bretherton, 1985).

Models with explicit ocean interior dynamics have resorted to a highly simplified, idealized geography on a single hemisphere, consisting of paired wedge-shaped continents and oceans that, starting at the pole, span 60° of longitude at the equator (Bryan *et al.*, 1982; Spelman and Manabe, 1984; Bryan and Spelman, 1985; Manabe and Bryan, 1985). To generalize results for the two hemispheres, this family of models imposes a condition of mirror symmetry at the equator. This severely limits the confidence with which results can be interpreted for the southern hemisphere, where the land/ocean ratio departs radically from 1 : 1 and continental effects are less prominent. In this context three comments are worth making: (i) The bi-hemispheric asymmetry of the climatic response in models with a realistic geographic setup is well established (Manabe and Stouffer, 1980); (ii) the contemporaneous instrumental record of temperature over the arctic and antarctic for the last 30 years shows that climatic trends for both regions are far from being symmetrical (Kelly, 1983); (iii) from another line of evidence, the paleoclimatological reconstruction of the surface of the ice-age earth (CLIMAP, 1976) generated a picture of sea-surface temperatures, ice extent, ice elevation and continental albedo, where bi-hemispheric differences were quite important.

Simulations in these models represent the asynchronous combined integration of three compartments: the atmosphere, the upper ocean (<1000 m) and the deep ocean (>1000 m), each of them reacting at their characteristic response time, i.e. because of the large heat capacity of the oceans, its response is quite slow compared with the atmosphere. Table I shows characteristic times to reach asymptotic equilibrium for each compartment in the simulations.

For short, 10-year time scales, ocean physics and air-sea exchange seem to control the capacity of the ocean to absorb increased atmospheric CO<sub>2</sub> levels. For longer time scales, however, chemical and biological processes play a decisive role in the cycling of nutrients, oxygen, sulphur and carbon (Shaffer, 1989; Shaffer and Sarmiento in print). The incorporation of bio-oceanographic processes, such as the carbon pump (McCarthy, 1985), into GCMs has been prevented so far by major uncertainties about the key processes and parameters involved.

### 2.1. *Asymptotic Equilibrium Under Normal CO<sub>2</sub>*

Asymptotic results for the oceans under normal CO<sub>2</sub> show general qualitative agreement with observed patterns. The model reproduces the main circulation patterns well: a subtropical anticyclonic gyre centred around 25° latitude with western boundary intensification; the across ocean eastward drift at the poleward edge of the subtropical gyre, splits into poleward and equatorward branches at the eastern boundary; a subarctic cyclonic gyre centred around 60° latitude (Bryan and Spelman, 1985). Calculated velocities, however, are weaker than measured values. Although the fields of salinity and temperature at the surface approximately reproduce the major patterns, they lack detail and miss some important features such as the huge temperature gradient at the edge of the western boundary current. Meridional sections of the ocean show that the distribution of isotherms lacks the characteristic equatorial doming and, generally, the model does not reproduce the equatorial thermocline well. The global thermohaline circulation that emerges displays mirror symmetry at the equator (Bryan and Spelman, 1985), in contrast to the highly asymmetric patterns of the Atlantic and Pacific Oceans (Reid *et al.*, 1978).

### 2.2. *Asymptotic Equilibrium Under Increased CO<sub>2</sub>*

The comparison between normal and increased CO<sub>2</sub> responses at asymptotic equilibrium (Spelman and Manabe, 1984; Figure 2) show that zonally averaged temperatures are higher everywhere compared with the normal climate. The warming in the deep ocean of 7.5 °C is about equal to the large warming of the ocean surface at 65°–70° latitude where oceanic stratification is weak and the heat anomaly can penetrate from the surface into the deeper ocean (Spelman and Manabe, 1984). Deep ocean warming is significantly greater than the one experienced by the surface layer expressed per unit area. The smallest temperature increase occurs in surface tropical waters, coinciding with the smallest atmospheric warming. In contrast with what happens in the atmosphere, the largest increase in temperature at the ocean surface does not occur at the pole (a distinct possibility in this model because of its geometry) but in a very shallow layer near 75° latitude. The explanation of this difference lies in the strong oceanic stratification observed at this latitude that partially insulates the surface water from the deeper ocean.

### 2.3. *The Transient Response*

Figure 3 shows the transient response of the same model after 25 years of warming following the sudden increase of CO<sub>2</sub>. Major results of these numerical experiments are: (i) the surface layer of the model atmosphere at high latitudes is almost decoupled from the ocean; (ii) near the sea-ice margin at 75° latitude, warming of the surface is limited to a shallow layer because the strong stratification caused by

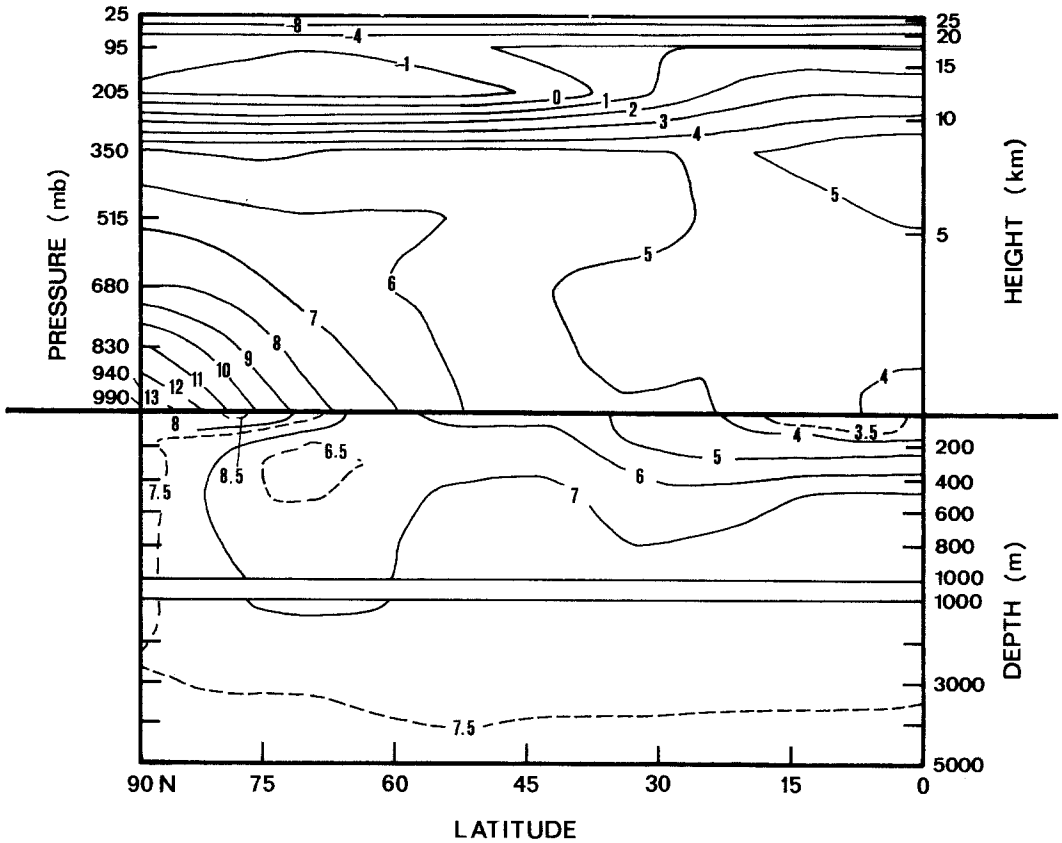


Fig. 2. Climate response to a fourfold increase of  $\text{CO}_2$ . Latitude height/depth distribution of the zonally averaged temperature change (Kelvin) at asymptotic equilibrium due to quadrupling the atmospheric  $\text{CO}_2$  content in the model with ocean currents. (Redrawn from Spelman and Manabe, 1984.)

the sharp halocline insulates deeper layers; (iii) maximal warming in the ocean occurs at subarctic (subantarctic) latitudes: around  $55\text{--}60^\circ$ ; (iv) the rate of penetration of surface warming into the deep ocean is exceedingly slow and has only a small influence upon the latitudinal distribution of zonally averaged temperature in the upper ( $<1000$  m) model ocean (Spelman and Manabe, 1984).

The surface circulation pattern established after 20 years in response to a fourfold increase in atmospheric  $\text{CO}_2$  (Bryan and Spelman, 1985) shows the presence of the subtropical anticyclonic gyre and two cyclonic gyres at higher latitudes, the latter a major difference on the normal pattern of circulation (Figure 4a); the distribution of salinity at the surface (Figure 4b) shows higher salinities in the subtropical anticyclonic gyre and two pools of very low salinity waters ( $<32\%$ ) close to the west and east boundaries caused by increased runoff from the continents.

Figure 5 shows the thermohaline circulation pattern. During the transient response period, water formed at the surface in high latitudes is not dense enough

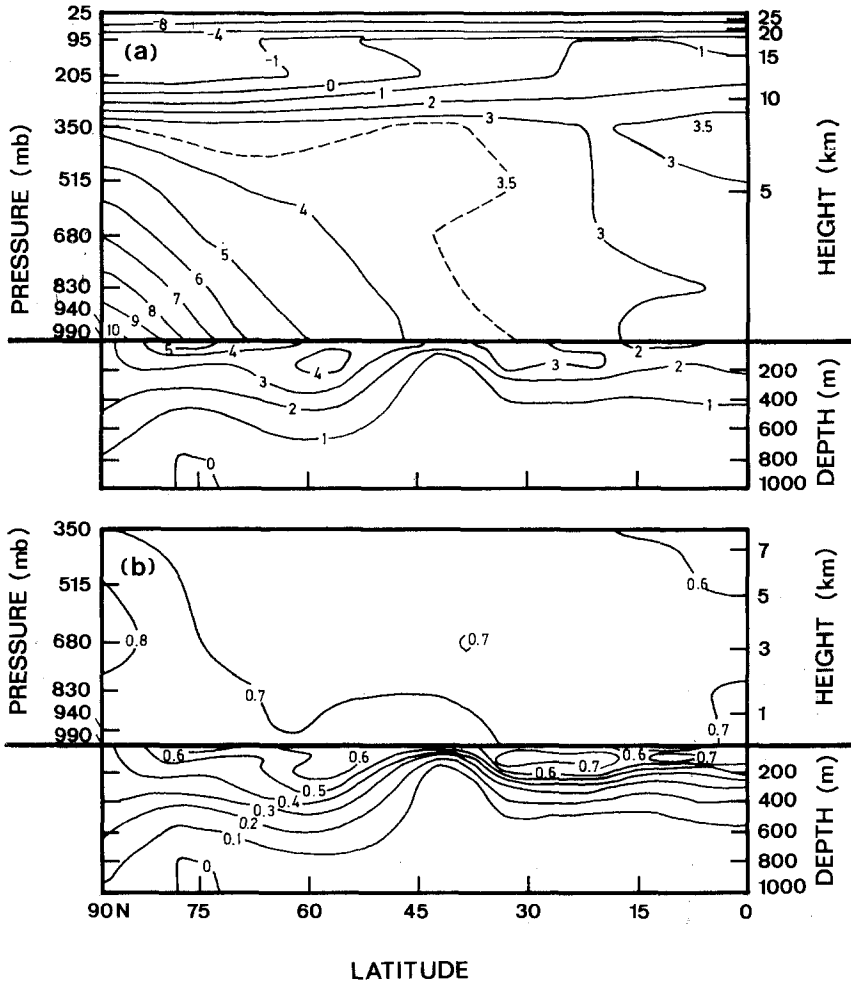


Fig. 3. The transient response after 25 years. Latitude height/depth distributions from the transient response study showing: (a) the zonally averaged temperature at 25 years minus initial temperature (Kelvin); and (b) the fractional response of zonally averaged temperature,  $R = [(T_1 - T_0)/(T_{as} - T_0)]$ , where  $T_{as}$  is the temperature at asymptotic equilibrium,  $R$  measures the fraction of the total response realized at the picture time. (Redrawn from Spelman and Manabe, 1984.)

to sink to the bottom and flows, as intermediate waters, toward the equator at mid depths (approx. 600 m). This leads to: (i) the formation of a clockwise cell in the deep ocean, and (ii) the shallowing and partial collapsing of the 'equilibrium' counterclockwise cell, that shows two nuclei at 25° and 60° latitude. The shallow cells induced by Ekman transport remain very much the same in all three cases of Figure 5 because zonal wind stress does not diminish after the onset of the increased  $\text{CO}_2$  conditions. Bryan and Spelman (1985) highlight the far-reaching consequences of the partial collapse of the thermohaline circulation, decreasing the ability of the ocean to take up  $\text{CO}_2$ .

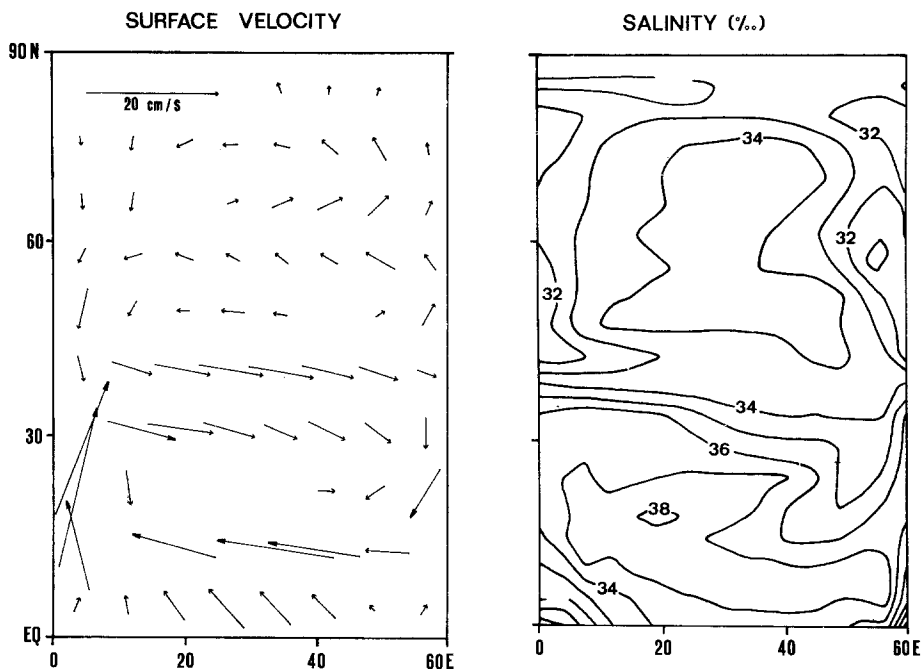


Fig. 4. Oceanic surface patterns during the transient period. **4a.** The surface current pattern corresponding to year 20 after 'switching on' increased  $\text{CO}_2$  conditions. Note the existence of two cyclonic gyres at high latitudes. Velocities in  $\text{cm s}^{-1}$ , maximal velocities at western boundary current. **4b.** The distribution of surface salinity in the transient regime after 25 years of 'switching on' increased ( $4\times$ )  $\text{CO}_2$  conditions. Note large pools of low salinity waters at both continental margins, indicative of increased run-off from continents. (Redrawn from Bryan and Spelman, 1985.)

Manabe and Bryan (1985) discussed a case where a sound, first order, prediction is not confirmed by model result. Following an increase of  $\text{CO}_2$ , the general warming of climate causes the reduction of meridional thermal gradients, a process exacerbated by the polar amplification phenomenon. This would suggest that meridional density gradients at the ocean surface should also decrease, debilitating the strength of the thermohaline circulation and diminishing the effectiveness of meridional heat transport by the oceans. However, numerical results show that the meridional density gradient at the ocean surface increases slightly with increasing  $\text{CO}_2$ . The explanation of this counter-intuitive result is simple: because the functional relationship between the thermal expansion coefficient of sea-water and temperature is highly nonlinear, at higher temperatures this coefficient is disproportionately increased. Therefore small changes in temperature of warm water, near the equator, cause similar changes in density to large increments in temperature of colder waters close to the poles.

Recently, Bryan *et al.* (1988) developed an improved version of the idealized geography model that uses an ocean basin differentiated into two hemispheres and preserves the actual ratio of continents and oceans. Figure 6 shows the asymptotic

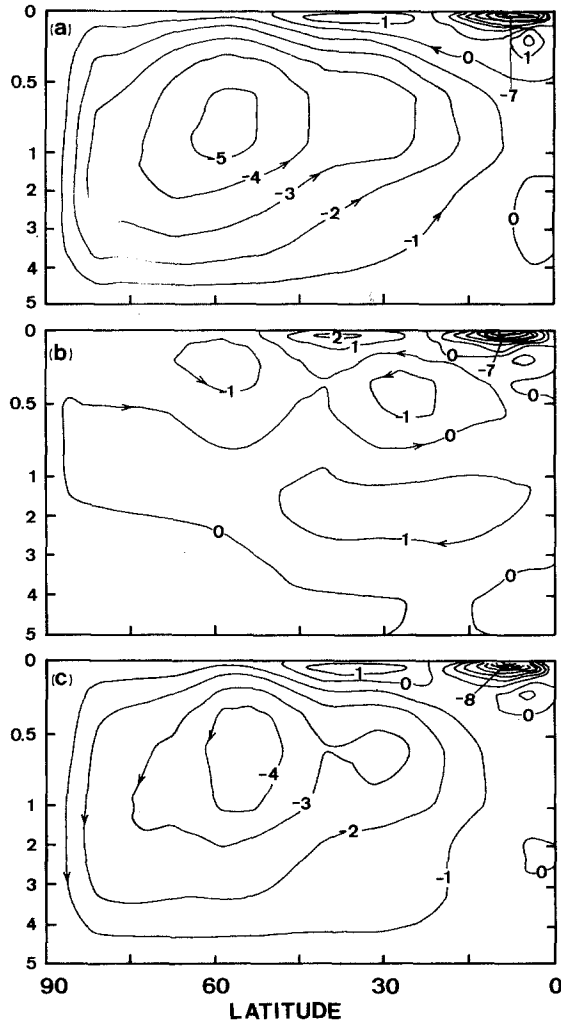


Fig. 5. The total meridional circulation. The zonally integrated equilibrium circulation, mostly thermohaline below the surface layer, in units of  $10^{12}$  g  $\text{seg}^{-1}$ : Overturning in the meridional plane shows a main counterclockwise circulation, with a concentrated downward branch near the pole and a broad upward branch close to the equator. Close to the surface, smaller circulation cells are associated with Ekman pumping/suction. Normal and increased  $\text{CO}_2$  simulations tend to show similar patterns, while the transient response after 20–30 years gives rise to radically different ones. (a) equilibrium solution for high  $4 \times \text{CO}_2$ ; (b) average circulation for years 21–30 after 'switching on', showing the partial collapse of the thermocline, reduced thermohaline circulation (<600 m) and a clockwise deep circulation; and (c) equilibrium solution for normal  $\text{CO}_2$ . Upper 1 km of ocean depth is expanded. (Redrawn from Bryan and Spelman, 1985.)

equilibrium result for the vertically and zonally integrated mass transport from this model under normal  $\text{CO}_2$ . The pattern of flow shown by the horizontal stream functions defines two subtropical gyres centred at  $30^\circ$ , clockwise in the north and counterclockwise in the south, and notably a strong circumpolar current between  $50\text{--}60^\circ$  S, with a total transport of  $120 \text{ Mt s}^{-1}$ .



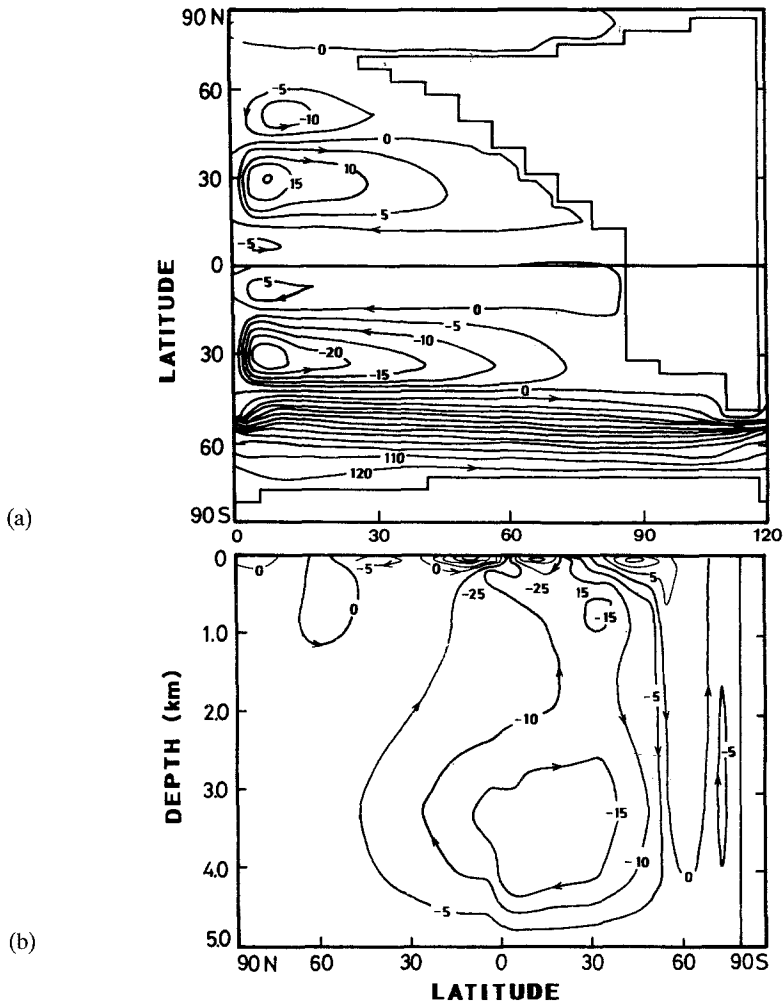


Fig. 6. Surface and meridional circulation patterns in the two-hemisphere models under normal  $\text{CO}_2$ . (a) The surface circulation pattern is shown by the streamlines of the vertically integrated mass transport in  $\text{Mt s}^{-1}$ : Dominant features are the circumpolar current with a total transport of  $120 \text{ Mt s}^{-1}$ , two subtropical gyres centred at  $30^\circ$  and the subarctic gyre. (b) The meridional circulation is shown by the streamlines of zonally integrated mass transport: The main deep cell is characterized by sinking in the Southern Hemisphere and rising motion in the Northern Hemisphere. Associated to the trades and westerlies, Ekman cells are observed in the surface layer. In the Southern Hemisphere the Ekman flow under the westerlies ( $40\text{--}45^\circ \text{ S}$ ) is compensated by a very deep cell ( $60^\circ \text{ S}$ ). (Redrawn from Bryan, Manabe and Spelman, 1988.)

The vertical meridional circulation is asymmetrical north and south of the equator. There are two Ekman cells associated with the trade winds that transport surface waters toward the poles and cause equatorial upwelling. The existence of the Drake passage in this model causes fundamental differences between the hemispheres: associated with the westerlies, Ekman transport is towards the equator.

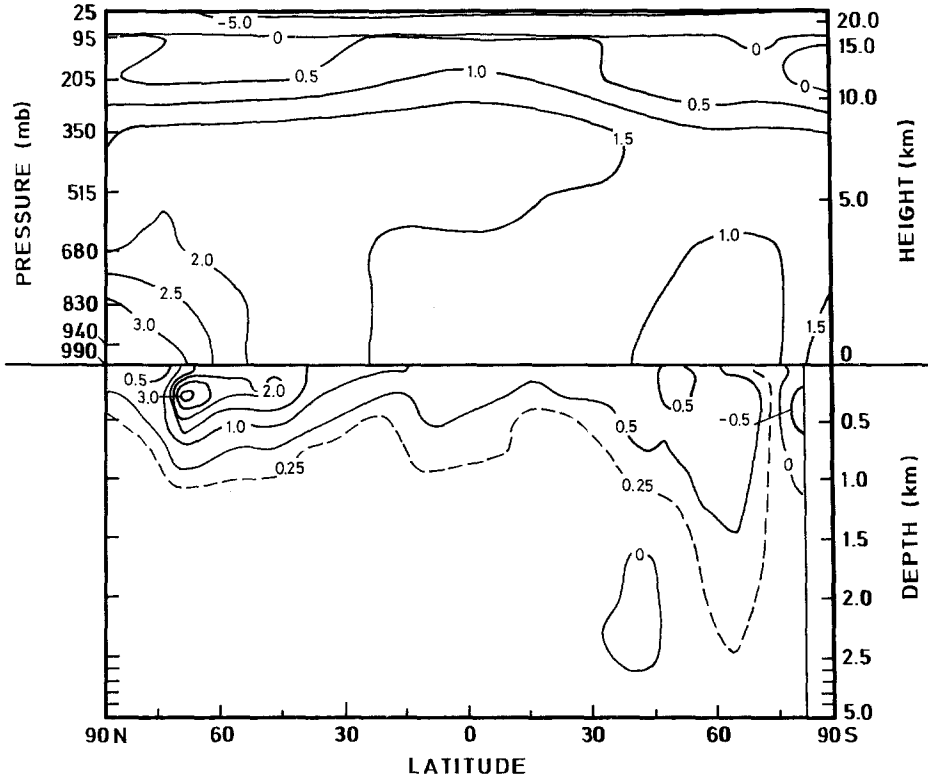


Fig. 7. The transient response after 41–50 years in the two-hemisphere model. Values are changes in temperature. A highly asymmetrical pattern emerges: Polar amplification, although strong in the equilibrium response (not shown), is much reduced during the transient period. Warming of the surface ocean is much less than predicted in the one-hemisphere model (Figure 3). Notice ‘cooling’ at the edge of the Antarctic continent. (Redrawn from Bryan, Manabe and Spelman, 1988.)

tor, and surface flow is compensated by a shallow return flow in the north and a very deep cell in the south.

Figure 7, from Bryan *et al.* (1988), shows the transient response of this model after 41–50 years of a sudden increase in  $\text{CO}_2$ . There is a clear asymmetry in the response of both hemispheres. The maximum upper ocean heating of 3.0 °C occurs around 60° N. Heating in the southern hemisphere is less than 1 °C and, surprisingly, after four decades, cooling (–0.5 °C) is observed close to the Antarctic continent. An interesting result is the deep penetration of the anomaly into the deep ocean in the south. Although with the exception of the cooling around Antarctica, these results are in general qualitative agreement with Spelman and Manabe (1984, see also Figure 3), and Manabe and Bryan (1985).

### 3. Effects of Climate Change on Marine Ecosystems

The physical changes predicted in the previous section will undoubtedly affect chemical and biological processes in the ocean. Some of these processes are part of climatic feedback mechanisms, notably the carbon cycle. Ultimately the drift of the climate system to a new equilibrium, following the perturbation introduced by increased atmospheric CO<sub>2</sub>, will necessarily involve chemically and biologically coupled processes. Predicting the global response of climate will call for models with explicit formulations of these feedback mechanisms, where the locations of sources and sinks of biologically active substances in the oceans will have to be considered.

#### 3.1. *Modelling the Global Biological Response in Marine Ecosystems*

Biological modelling of the oceans has proceeded in two directions: (i) elucidating single processes, such as the relationship of primary production and light, or the incorporation of nutrients by phytoplankton; and (ii) developing coupled processes models of the trophic level type (Steele, 1974). However, these models have restricted spatial coverage, limited to local, mesoscale (Walsh, 1975; Wroblewski, 1977) or regional (Hofmann, 1988) scales, and until very recently no attempt had been made to model the large scale biological response with a spatial resolution commensurable with GCMs. Wroblewski *et al.* (1988) published a basin-wide climatological solution of a plankton dynamics trophic level model with a resolution of 1°, for the month of May in the North Atlantic. Comparison of the results with a composite of CZCS chlorophyll images permit reasonable interpretations of the observed patterns in terms of the internal dynamics of the model.

As stated before, the physics does control the changing climate in the short term (10–20 years), but global modelling incorporating biospheric processes will be mandatory for longer term prognosis. At longer time scales, chemical and biological processes (primary production, denitrification) have been successfully invoked to explain paleoclimatic changes in the Quaternary. Shaffer (1989) produced a biogeochemical model relating the bi-hemispheric rapid terminations of ice ages and their 100 000 year periodicity to oscillations in oceanic primary production controlled by nutrient availability. Ice-age terminations result from denitrification events at mid-depths and 100 000 year periods derive from the internal response of the model given the present width and shape of the continental shelf. In this model oscillations are started by moderate drops in sea level which trigger shelf erosion events that trap/release nutrients. In this context, understanding high latitude dynamics becomes a primary goal: the ventilation of the deep ocean through the interchange of CO<sub>2</sub> and oxygen between ocean and atmosphere at the site of formation of dense bottom water near the Antarctic continent.

### 3.2. Evidence for Climate-Induced Changes in Marine Ecosystems

The search for climate-related changes in marine populations and fisheries is an old and recurrent topic in marine ecology (for a review see Cushing, 1982). This is considered by many as an intellectually risky endeavour, to say the least, since in most cases no clear mechanisms are implied, and conclusions are based exclusively on

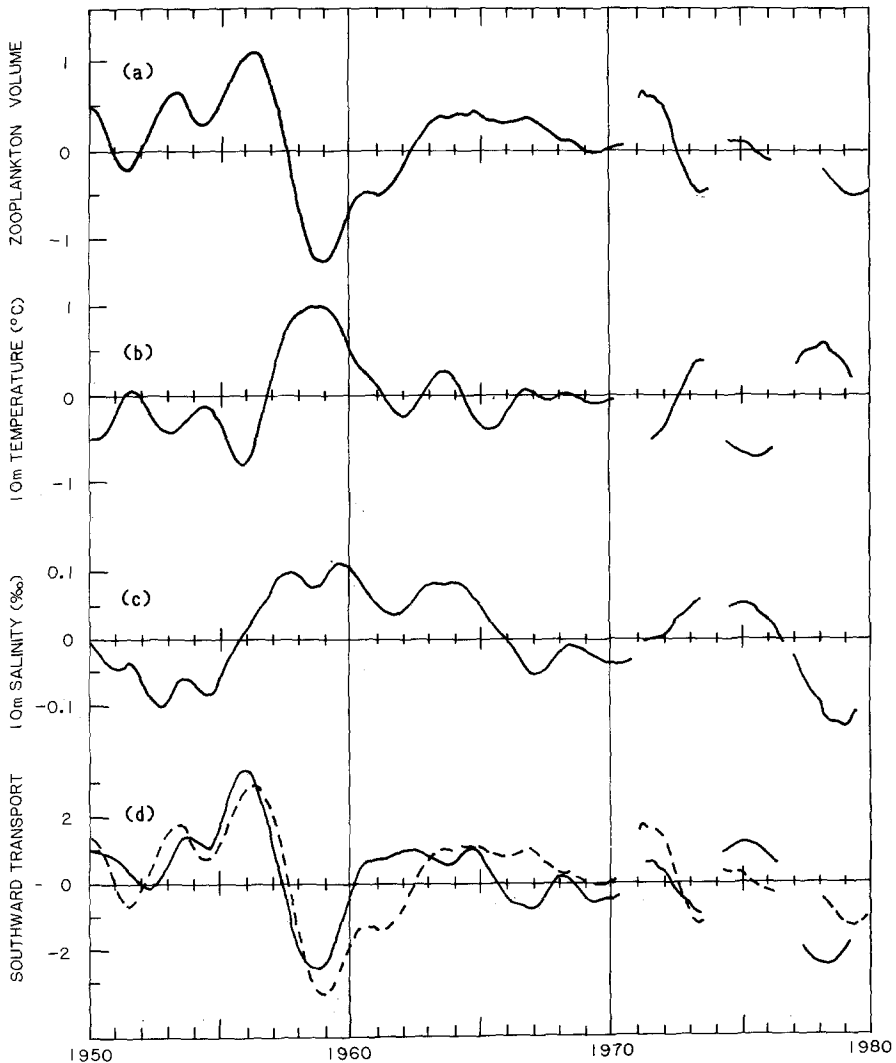


Fig. 8. Interannual variability in the California Current. Time series (monthly intervals) of: (a) zooplankton biomass in  $\log_e(\mu\text{m}^{-3})$ ; (b) the average temperature at 10 m in  $^{\circ}\text{C}$  over 150 hydrographic stations; (c) the average salinity (%) at 10 m over the same stations; (d) amplitude of the principal orthogonal function of the  $^{\circ}_{500}$  decibars (anomalous) steric height, dashed line reproduces the zooplankton curve. (From Chelton *et al.*, 1982.)

empirical correlations. Furthermore, the state of knowledge about the internal structure of marine ecosystems limits our ability to predict changes induced by external driving functions, such as climate. Despite these limitations, we review some cases where there seem to be good reasons to ascribe part of the variability of the observed response of marine ecosystems to climate. Studies showing large-scale, low-frequency changes in marine ecosystems are few because, except fishery data that accumulates as a by-product of industrial operations, obtaining extensive data bases or long time-series of biological variables is extremely expensive and labour intensive. The development of automated instrumentation and the acquisition of remote sensing capabilities might improve the situation in the future.

Bernal (1979, 1981) and Chelton *et al.* (1982) discuss the large and widespread changes in the secondary production of the epipelagic ecosystem of the California Current using the CalCOFI data bases from 1949 to 1980 (Figure 8). In the inter-annual time scale, changes are associated with warming/cooling events lasting around 2 to 3 years. The largest fraction of the variability of these low-frequency changes is strongly associated with large-scale changes of an advective component of the flow, partly related to ENSO. Changes in advection (of remote origin) induce local changes in the availability of inorganic nutrients, generating a local response of the ecosystem through new production. Some observed events are clearly linked to ENSO; however, others seem to be related to the intensification/weakening of the anticyclonic gyral circulation resulting from basin-wide changes of the atmospheric torque.

Colebrook, using the extensive Continuous Plankton Recorder data base from 1948 to the present, in a series of papers (Colebrook, 1972, 1978, 1985) has documented large-scale changes in zooplankton abundance, seasonality and composition in the North-East Atlantic and the North Sea. The most remarkable event in this region has been the delayed time of onset of the spring bloom. During a period of thirty years the production cycle was delayed by about three to four weeks, simultaneously the seasonal production of zooplankton biomass has gradually been reduced from seven or eight months to about five or six months (Cushing, 1982). Furthermore, total zooplankton biomass in the North-East Atlantic and North Sea followed a monotonically decreasing almost linear trend (Figure 9) that in 28 years reduced the total biomass by about half. Climatic correlates for these changes are the wind strength and direction and horizontal advection (i.e. changes in the north Atlantic current). As Colebrook (1978) states the case, 'this will imply that about half of the observed variability in the annual means can be attributed to density-independent, physical environmental processes.'

Harris *et al.* (1988) studied a time series of sea surface temperature off Tasmania and found significant interannual variability closely associated to the intensity and duration of the zonal westerly winds. This series seems to be a good index of a climatic syndrome that has clear correlates in the pressure fields, rainfall patterns and water level changes in local lakes over the region. Fresh-water fish recruitment seems to be influenced by this strong climatic signal, as is the population size of

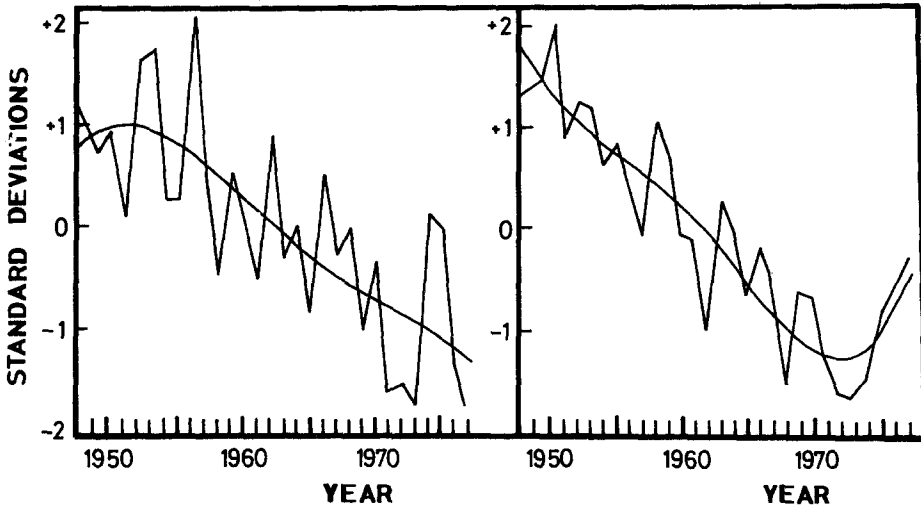


Fig. 9. Total zooplankton biomass between 1948 and 1974. Figures show the reduction in total zooplankton biomass in the north Atlantic (left) and the North Sea (right) during a period of 26 years. (Redrawn from Cushing, 1982.)

spiny (rock) lobsters at both sides of the Tasman Sea. These authors highlight the fact that the correlation between surface temperature and population size is of opposite sign for species of lobster that live north and south of the Subtropical Convergence Zone.

### 3.3. *The Changing Climate Scenario of the Oceans*

Since the warming of the ocean will first comprise a shallow surface layer, smaller oceanic reservoirs will be affected first by climatic changes and consequently time scales involved will be short, in the interdecadal range. Therefore it is reasonable that transient responses (Figures 3, 4, 5 and 7) will dominate the changing climate scenario in the oceans.

This scenario suggests warming of the surface layer up to 3 to 4 °C at middle latitudes. This means an extension of tropical conditions toward the poles and shifting of surface water masses boundaries. Benthic intertidal communities should receive the immediate impact of these changes. Pools of low salinities would appear close to continental boundaries, caused by increased run-off from continents, representing a new source of inorganic nutrients. This will change the distribution of areas supporting high primary production. In the next paragraphs, I will briefly sketch some of these potential impacts on marine ecosystems.

(i) *Coastal and oceanic islands:* Island habitats will experience drastic modification following the changes taking place in their surrounding waters. Specially important are the potential changes in the productivity around some oceanic

islands that could diminish their general carrying capacity, affecting resident populations of species that have limited mobility, such as colonial birds and mammals. This is an important aspect to be considered from the point of view of preservation of biodiversity.

(ii) *Expansion/contraction of pelagic habitats:* One of the important direct effects of climatic changes in the ocean will be the expansion/contraction of epipelagic and pelagic habitats, affecting the distribution, production and local survival of organisms. For truly pelagic species this might seem to be an almost trivial mechanism, irrelevant for many large organisms. In most marine species, early stages of their life cycles are small, fragile and planktonic. Early life history stages of fish are a good example. Most of them live in the surface layers, though they might live further down in the water column as adults, like the mesopelagic members of the Family Myctophidae. The ecology of fish larvae is considered to play a key role in the regulation of fish populations through controlling recruitment to adult populations. During these early life stages, larvae are exposed to different mortality factors such as predation, starvation, and emigration from optimal environments (Lasker, 1975; Sinclair *et al.*, 1985). Small changes in temperature could enlarge/restrict to a significant extent the oceanic areas where successful larval survival occur. Larval retention areas (Iles and Sinclair, 1982) depend on the existence of rather precise circulation patterns that may be altered. On the other hand, warming of the surface layer will increase stratification and, if other factors remain equal, this change should enhance the formation of layers of high concentration of food particles, and extend their area of occurrence. These layers are a key, limited resource for fish larvae survival, since average concentrations of particles in the ocean do not provide enough food for maintaining a positive daily energy budget for the larvae.

(iii) *Pelagic fisheries:* The expansion/contraction of habitats will not only affect small or juvenile animals. Sharp (1987) has called attention to the transient increase and decrease of the catch rate of tuna in the eastern tropical Pacific, associated with the onset/offset of ENSO. Here the mechanism involved is the shallowing/deepening of the thermocline; 'the tuna habitats are diminished in depth, and they become more visible and more vulnerable to surface fishing gear' (Sharp, 1987). A monotonic trend toward a shallow thermocline would make these changes more permanent and pronounced, having a larger effect on the ecology and fisheries of tunas and similar pelagic species. The effect described for tunas by no means applies exclusively to these visual predators. The reduction in size of habitats will necessarily increase the rate of intra- and interspecific encounters, and potentially could exacerbate competitive and predatory interactions among many pelagic species.

(iv) *Ocean-wide distributional changes:* The distribution of planktonic communities in the ocean does conform to a stable biogeographical pattern that is regulated

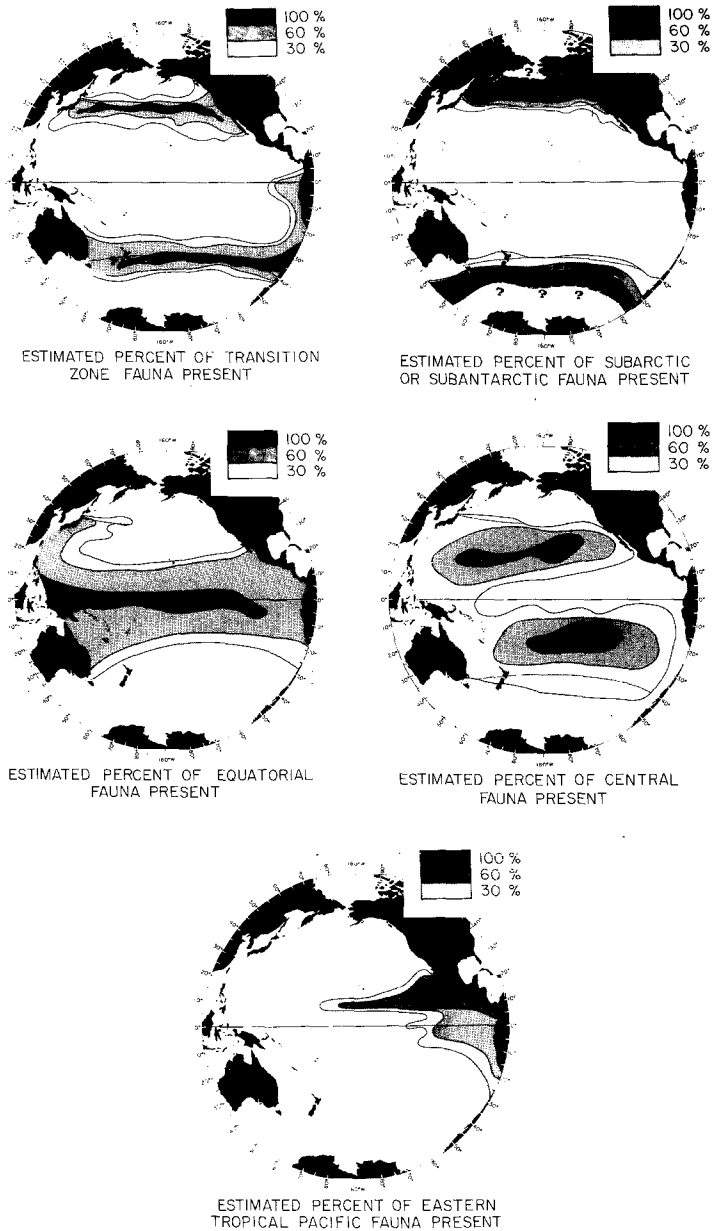
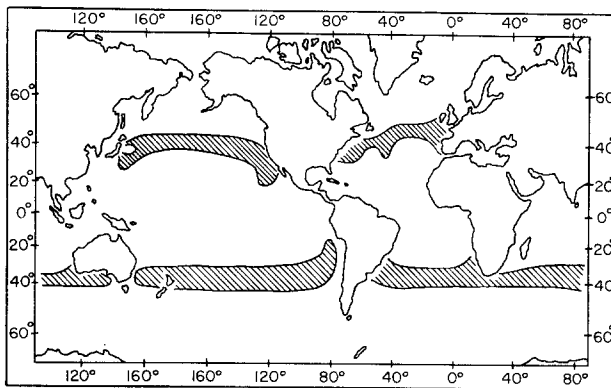
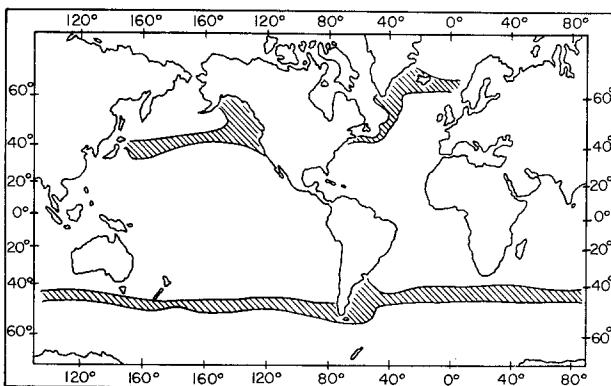


Fig. 10. Major biogeographical patterns in the Pacific Ocean. These patterns were determined by overlapping maps of the biogeographic distribution of many species of zooplankton and two groups of pelagic organisms: ommastrephid squid and tuna. Contours and shades represent the estimated percent of each regional fauna present within the boundaries. The 100% contour indicates that a 'pure' fauna is present, therefore, contour intervals are in order of decreasing fidelity to the central core of each fauna. (from McGowan, 1974.)

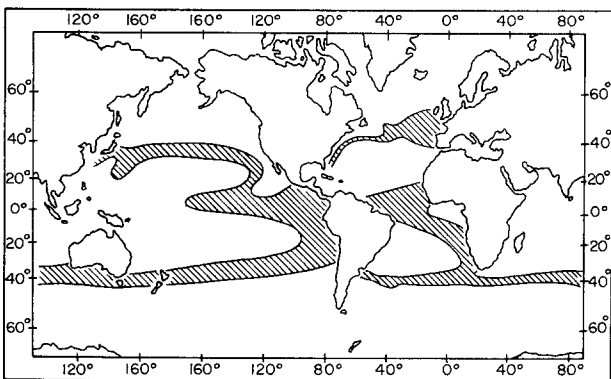




a. *Thysanoessa gregaria*, present distribution



b. Postulated distribution, with 2 1/2° warming (at 200 m.)



c. Postulated distribution, with 2 1/2° cooling (at 200 m.)

Fig. 11. Distributional changes of a species of Euphausiid. The hypothesized distribution of *Thysanoessa gregaria* for 2.5 °C increment or decrement in temperature at 200 m: (a) actual distribution; (b) warm conditions; (c) cold conditions. (From Brinton, 1962.)

by major circulation systems (McGowan, 1971, 1974). This pattern is very old, and, based on several lines of evidence, it has been established that in the Pacific Ocean it 'has been the same for several tens of millions of years' (McGowan, 1974). Figure 10 shows five of these characteristic patterns for the Pacific Ocean. At the species level, it has been suggested by Brinton (1962) that the biogeographical boundaries of some Euphausiids might have changed in the past, in response to warming/cooling events, a mechanism that might have contributed to their speciation. In Figure 11 the hypothetical distributional changes that *Thysanoessa gregaria* might experience in response to a warming/cooling of 2.5 °C is shown. This simple approach can be useful to explore some consequences of global warming, since similar maps can be generated for epipelagic species using the predicted temperatures of the surface layer of the ocean for the next thirty years. The patterns of circulation predicted to happen during the transient period (Figure 4) by this generation of physical models, if confirmed by future, more realistic ones, would radically modify the distributional pattern of subarctic, subantarctic and transitional species (McGowan, 1974).

(v) *Primary production*: Of dynamic processes, primary production is essential, not only because it is the first link in the transfer of energy in marine ecosystems, but because it also plays a key role in the biological pump of carbon in the oceans. As mentioned above, the least known physical process in the ocean is mixing. Mixing plays a fundamental role for primary production, because it is the supply of nutrients to the euphotic zone, a rate process which controls primary production. Although a general warming, according to our knowledge of the physiology of phytoplankton, should increase the rate of production (photosynthesis), if the supply of nutrients remains unchanged, a faster turnover rate would exhaust nutrients earlier, but would not increase net production. A warming of two degrees seems trivial when one compares the integrated production of the warm oligotrophic central gyres with the cold coastal upwelling areas in eastern boundary currents. However, if warming increases stratification, as it should, mixing would diminish and the supply rate will fall. But, if run-off increases, as predicted by the model at intermediate latitudes, this allochthonous, new input of nutrients by rivers, should increase production. This might happen in the warmed oceans of the transient period. Figure 4b shows the surface distribution of salinity after 20 years of 'switching-on' the increased CO<sub>2</sub> atmosphere. Large pools of very low salinity water are seen close to the continental margins between 40 and 60° latitude in the western boundary and between 40 and 80° latitude in the eastern boundary. If one recalls that, according to the physical models, these latitudes will experience a significant warming, the enhanced physiological response of the phytoplankton, supported by a new source of nutrients from run-off, could give rise to a truly 'hot spot' of primary production at these latitudes, a feature unknown in today's oceans.

### 3.4. Conclusions

There is little doubt that following the increase of CO<sub>2</sub> in the atmosphere, climatic changes involving the world oceans will occur in the next 50 years. Despite the success in modelling global climate, exact prognosis of these changes for the oceans is difficult because of the state of knowledge on some key oceanic processes. However, in addition to the direct climate feedback mechanisms that the marine biosphere and ocean circulation provide, the oceans will be affected, altering the pattern of distribution of conservative properties and its circulation. In turn these changes will modify the biodynamic of production and the distributional patterns of marine populations. Together with current efforts to improve our understanding of the complex interaction between the climate and the biosphere, this aspect of climate change, because of its importance and potential impact on economic activities, such as coastal and oceanic fisheries, deserves further consideration on its own merits.

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