

ROLE OF MARINE PELAGIC ECOSYSTEMS WITH REGARD TO BIOLOGICAL RESOURCES IN OCEANS AND GLOBAL CLIMATE CHANGE

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RESUM

En aquest article es discuteix la importància que tenen les interaccions entre la hidrodinàmica i els processos dels ecosistemes pelàgics en la canalització del carboni biogènic dels oceans. Aquestes interaccions i processos influencien en gran mesura la disponibilitat dels recursos biològics i també el segrest del carboni biogènic, el qual té un paper significatiu en el canvi climàtic global. Es discuteixen els conceptes de reciclatge de carboni, exportació i segrest, i bombes de CO₂ biològic, en relació amb els de producció nova i regenerada (model estequiomètric/estadi estacionari). En el context d'un model conceptual de producció/exportació des de la zona eufòtica, s'arriba a la conclusió que les particularitats hidrodinàmiques són el factor clau de control de la bifurcació que condueix al reciclatge o a l'exportació de la producció pelàgica primària. Contràriament a les suposicions del model estequiomètric/estadi estacionari, es fa una revisió de quatre casos generals, on es mostra que els ecosistemes pelàgics poden tenir un efecte significatiu en l'exportació i segrest del carboni biogènic en els oceans.

La dinàmica dels ecosistemes marins pot, per tant, jugar un paper important en la canalització del carboni biogènic en les vies d'exportació, i això condueix a recursos vius explotables o, eventualment, al segrest addicional del carboni. Les floracions de microalgues marines són una dada per a la comprensió del paper dels ecosistemes pelàgics marins. Està demostrat que, si bé les floracions no aporten cap informació sobre la producció primària, en canvi sí que són significatives en el destí de la producció primària dins de l'ambient marí (important per les pesqueres i l'exportació de partícules biogèniques des de la zona eufòtica).

Es descriu una tipologia de l'ecosistema pelàgic marí des de diverses combinacions de producció i biomassa de fitoplàncton marí: com a dominació d'una gran nombre de cèl·lules petites o de cèl·lules grans. Es descriuen les principals característiques dels cinc tipus d'ecosistemes en relació amb les pesqueres i l'exportació del carboni biogènic. Finalment, es classifica el carboni biogènic en els oceans en relació amb la taxa de renovació del carboni biogènic. Es discuteixen, amb referència als cinc tipus d'ecosistemes pelàgics marins i al control exercit per l'ambient d'aquests ecosistemes, les tres fonts de carboni biogènic en els oceans (amb punts de trencament de 10⁻² i 10² anys). Es proposa que el control ambiental de les diferents reserves de carboni biogènic depèn de la quantitat d'energia auxiliar (p. ex., mecànica) que és subministrada a l'ambient pelàgic. Es conclou que, d'acord amb la naturalesa de les interaccions entre la hidrodinàmica i les propietats de l'ecosistema, el carboni fosfosintèticament pot ésser canalitzat per vies de vida curta, de vida llarga o pot ésser segrestat.

MOTS CLAU: oceans, fitoplàncton, carbó biogènic, segrest.

SUMMARY

The central thesis of this paper is that, in the oceans, interactions between hydrodynamics and processes of pelagic ecosystems play a major role in channeling the flux of biogenic carbon. This influences to a large degree the availability of biological resources, and also the sequestration of biogenic carbon, which is of significance with regard to global climate change. Concepts of carbon recycling, export and sequestration and of the biological CO₂ pump are discussed in relation with those of new and regenerated production (steady-state/stoichiometry model). Within the context of a conceptual model of production export from the euphotic zone, it is concluded that hydrodynamic singularities are a key factor controlling bifurcations that lead to either recycling or export of pelagic primary production. Contrary to assumptions underlying the steady-state/stoichiometry model, four general cases are reviewed showing that pelagic ecosystems may have a significant effect on the export and sequestration of biogenic carbon in oceans. The dynamics of marine ecosystems may thus play an important role in channeling biogenic carbon into export pathways, that lead to exploitable living resources or eventual sequestration of carbon. Blooms of marine microalgae provide additional insight into the role of marine pelagic ecosystems. It is showed that blooms provide little, if any information on primary production, their true significance mainly concerning the fate of primary production in the marine environment (which is of importance for both fisheries and the export of biogenic particles from the euphotic zone). A typology of marine pelagic ecosystems is designed from the various combinations of phytoplankton production and standing stock, as dominated by large small cells or resulting from a combination of various cell sizes. The main characteristics of the five types of ecosystems are described, with regard to fisheries and to the export of biogenic carbon. Finally, biogenic carbon in oceans is classified by reference to the turnover rate of biogenic carbon. The three pools of biogenic carbon in oceans (with break points at 10⁻² and 10² years) are discussed within the context of the five types of marine pelagic ecosystems, and also by reference to the control exerted by the environment on these ecosystems. It is proposed that the environmental control of the various pools of biogenic carbon depends on how auxiliary (i.e. mechanical) energy is delivered to the pelagic environment. It is concluded that, according to the nature of the interactions between hydrodynamics and ecosystem properties, the photosynthetically fixed carbon may be channeled into either short-lived or long lived-pathways or become sequestered.

KEY WORDS: *oceans, phytoplankton, fisheries, biogenic, carbon, sequestration.*

INTRODUCTION

This paper summarizes a number of ideas published in the past few years by the author, alone or in collaboration. The central thesis is that, in the oceans, interactions between hydrodynamics and processes of pelagic ecosystems play a major role in channeling the flux of biogenic carbon. This influences to a large degree the availability of biological resources and also the sequestration of biogenic carbon, the latter being of significance with regard to global climate change (re.greenhouse effect). For the sake of concision, detailed

references are not given hereinafter but these can be found in publications listed in the bibliography.

One of the most pressing issues presently confronting the scientific community, worldwide, is the possible rapid global warming of the Earth. The recent anthropogenic increase in atmospheric carbon dioxide may be responsible for about half this global warming. It has been estimated that up to about half the CO₂ released since the beginning of the industrial era may have been absorbed by the oceans (Sundquist, 1985). Carbon dioxide transferred into the deep oceanic waters is effectively re-

moved from the atmosphere for centuries, thus reducing the magnitude of global warming.

Another area of growing concern for the scientific community is the present state of exploited marine renewable resources. Many authors have pointed out that the models used for stock management are inadequate, and that the general relationship between primary production and fish yield, which is probably mediated by the success of larval recruitment to the adult population, still eludes understanding, potentially leading to overexploitation. In addition, the increasing frequency of exceptional phytoplankton blooms may imperil coastal fisheries and aquaculture operations. Recent papers (Parsons and Lalli, 1988; Cushing, 1989; Iverson, 1991) indicate that one of the key factors in the control of exploited marine populations may be phytoplankton production and its export pathways.

Export and sequestration of biogenic carbon in oceans

A fraction of the carbon fixed by microalgae in the upper ocean is transferred out the euphotic zone. This includes sinking biogenic particles, advected dissolved organic compounds and also material passed on to the food web (Legendre and Le Fèvre, 1991). Biogenic material may end up being transferred from the production area either horizontally, through passive transport associated with circulation or active migration of large animals, or vertically, again passively, through sedimentation of living or detrital particles, or actively, through vertical migrations.

Within the context of global climate change, two concepts must be distinguished concerning the fate of biogenic carbon in oceans, i.e. export and sequestration. *Export* refers to the flux of biogenic material from surface waters to depth, while *sequestration* concerns the removal of dissolved inorganic CO_2 from the atmosphere

and surface waters for periods of interest to global warming (i.e. at least a few hundred years). Export of biogenic carbon and sequestration of carbon are generally not equivalent, since a large fraction of the exported biogenic carbon may be rapidly respired during its downward transit and recycled back to the atmosphere. For global biogeochemical budgets, the really significant term is not the export but the actual sequestration of carbon. Volk and Hoffert (1985) indentify three CO_2 pumps in the oceans, one physical and two biological. The *solubility pump* (physical) is associated with ocean circulation. It is especially active in areas of deep water formation (polar regions), where cooling of the surface water drives a flux of CO_2 from the atmosphere to the ocean, and subsequent sinking of the water ensures sequestration of the dissolved inorganic carbon; this will not be discussed in the present paper. One biological pump exports carbonate (the *carbonate pump*), and its overall effect on the sequestration of atmospheric CO_2 may be rather complex, as briefly explained below. The other (the *soft-tissue pump*, also known as the *biological CO_2 pump*) plays an important role in the export of biogenic carbon, of which a fraction may be sequestered. The relative importance of biological versus physical pumping of CO_2 in the oceans is presently under debate (e. g. Broecker, 1991).

The steady-state/stoichiometry model

Biological oceanographers often distinguish between two types of phytoplankton production: (i) new production (P_N), which is derived from allochthonous nutrients, and (ii) regenerated production (P_R), which is fueled by autochthonous nutrients locally regenerated by heterotrophs. The importance of P_N versus P_R is usually estimated from the relative uptake by phytoplankton of NO_3^- versus NH_4^+ and also sometimes urea, generally using ^{15}N -labelled tracers (Dugdale and Goering, 1967). Total primary productions is $P_T = P_N + P_R$, and the ratio

of new to total production («f-ratio») is $f = P_N / P_T$. The concepts of new and regenerated production refer to the origin of nutrients used by the primary producers, not directly to the fate of primary production in marine ecosystems. In the present paper, «recycled production» and «export production» are used to identify pathways in the food web.

It is often assumed, at least implicitly, that the biological CO_2 pump is essentially driven by the upward flux of NO_3^- (Fig. 1), so that the potential export of biogenic carbon from the upper ocean would be stoichiometrically equivalent to phytoplankton new production (Eppeley and Peterson, 1979). This approach assumes that ecosystems are in a steady-state condition over

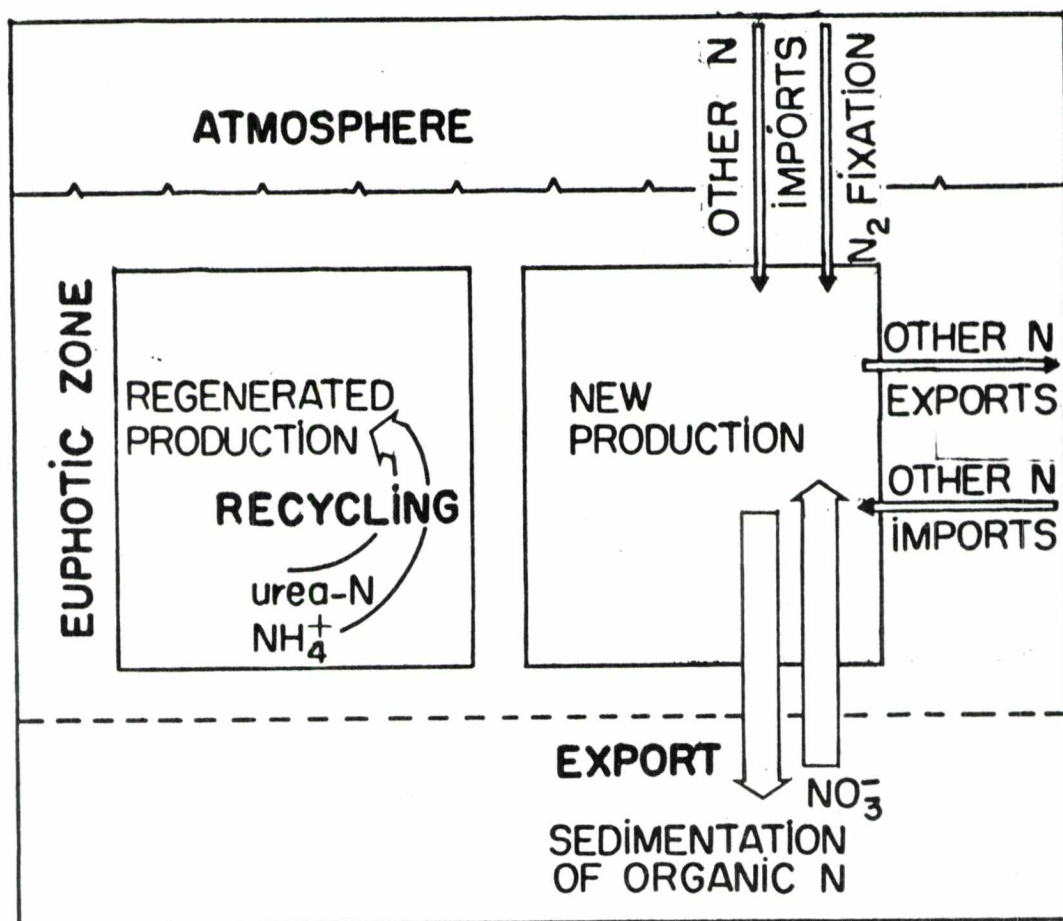


FIGURE 1. Schematic diagram of the steady-state/stoichiometry mass-balance model for new (P_N) and regenerated (P_R) phytoplankton production. In this model, P_R is fueled solely by nutrients regenerated within the euphotic zone, while P_N depends on the supply of allochthonous nitrogen (essentially the flux of nitrate from depth). Under steady state, the upward flux of nitrate should be balanced by the downward flux of nitrogen in sedimenting particles. Adapted from Platt *et al.* (1989).

the significant spatio-temporal scales. However, it is recognized (Platt *et al.*, 1989) that the assumption of a dynamic steady state is no more than an idealisation of a system that, in reality, is perturbed intermittently such that the condition of instantaneous equilibrium is rarely, if ever, attained. In fact, the very concept of global climate change denies steadiness on relevant scales (Legendre and Gosselin, 1989). The model also implies that variations in the proportion of carbon and nitrogen assimilated (and released) by marine plankton only have short term relevance and that the stoichiometric balance is conserved at the steady-state scale. The stoichiometric equivalence would follow the Redfield ratio, i.e. in terms of atoms C:N:P = 106:16:1 (C:N = 6.6) which corresponds to the average cellular composition of marine plankton. Finally, the model does not consider that ecosystem dynamics have a significant influence on the export or sequestration of biogenic carbon. Given a certain upward flux of nitrate, it is assumed that there will be a proportional downward flux of biogenic carbon, if the fluxes are integrated over proper spatio-temporal scales (Platt *et al.* 1989). Assumptions underlying the model will be discussed below, and alternative approaches proposed.

EXPORT AND SEQUESTRATION OF BIOGENIC CARBON IN OCEANS: HYDRODYNAMIC CONTROL AND PELAGIC ECOSYSTEMS

Hydrodynamic control of production export in oceans

Legendre and Le Fèvre (1989) point out that the oceanic environment is characterized by the presence of hydrodynamic singularities, that occur over a wide range of spatio-temporal scales.

Examples of such singularities are: (i) on the vertical axis, the pycnocline and the ice-water interface; (ii) on the horizontal plane, eddies, fronts, upwelling areas, and coastal zones; (iii) along the time axis, temporal transitions in vertical stability of the water column with periodicities ranging from annual to semidiurnal (tidal) and sometimes smaller (e.g. Langmuir circulation). Their hypothesis is that hydrodynamic singularities play a major role in favouring production export over in situ recycling.

Legendre and Le Fèvre (1989) discuss the role of hydrodynamic singularities within the framework of a conceptual model, where five major bifurcations are specified (Fig. 2). The first bifurcation differentiates between the production of large (> 5µm, including chains of small cells) versus small cells (< 5µm; ultraplankton). According to Stokes' law (see Margalef, 1978), large cells should sink rapidly (*sedimentation pathway*). However, under certain conditions (bifurcation 2), these cells are retained within the euphotic zone, where they may either (bifurcation 3) be grazed by herbivores (*herbivory pathway*) or accumulate in hydrodynamic traps where they eventually degrade into smaller particles before being grazed by microphagous feeders (*detritivory pathway*). Unlike the large cells, most of the ultraplankton remain in the euphotic zone where they are generally recycled in the microbial food loop (ultraplankton → heterotrophic bacteria → protozoa) within which most of the stored energy may be dissipated. Direct escape from this loop is possible, through «baleen-whale» feeding of large metazoans (e.g. appendicularians) grazing directly on bacterial size plankton. Bifurcation 4 gives conditions under which very small cells may escape the microbial food loop, either directly (*baleen whale feeding pathway*) or through aggregation into larger particles. These aggregates may then (bifurcation 5) either sediment (*marine snow pathway*) or accumulate in hydrodynamic traps (microphagy, *detritivory pathway*; re.bifurcation 3). The

authors show that hydrodynamic singularities are involved in the five bifurcations.

At each bifurcation, part of the primary production may be channeled into export pathways, which does not preclude coexistence with recycling pathways. In fact, recycled production takes place at each bifurcation in Fig. 2, where the ratio of recycled to total production increases from left to right in the diagram. Production and sinking of large cells (bifurcation 1) is accompanied by exudation of organic matter in the euphotic zone, at a rate considered rather small by some authors while others quote values up to 50% of the net annual production. Bifurcation 2 leads to grazing by herbivores, and therefore to excretion of

dissolved organic matter in the euphotic zone. Bifurcations 3 and 5 converge toward the accumulation biotope, where probably more than 85% of the biomass is recycled. Export of ultraplankton through sinking is only possible if the cells are incorporated into large organic aggregates, in which recycling by bacterial activity is very high. Finally, small cells in the microbial food loop (bifurcation 4) are almost entirely recycled.

The authors conclude that hydrodynamic singularities are a key factor controlling bifurcations that lead to either recycling or export of pelagic primary production. The significance of this conclusion follows from the fact that the fates of recycled and export production are not the same either ecologically or geologically.

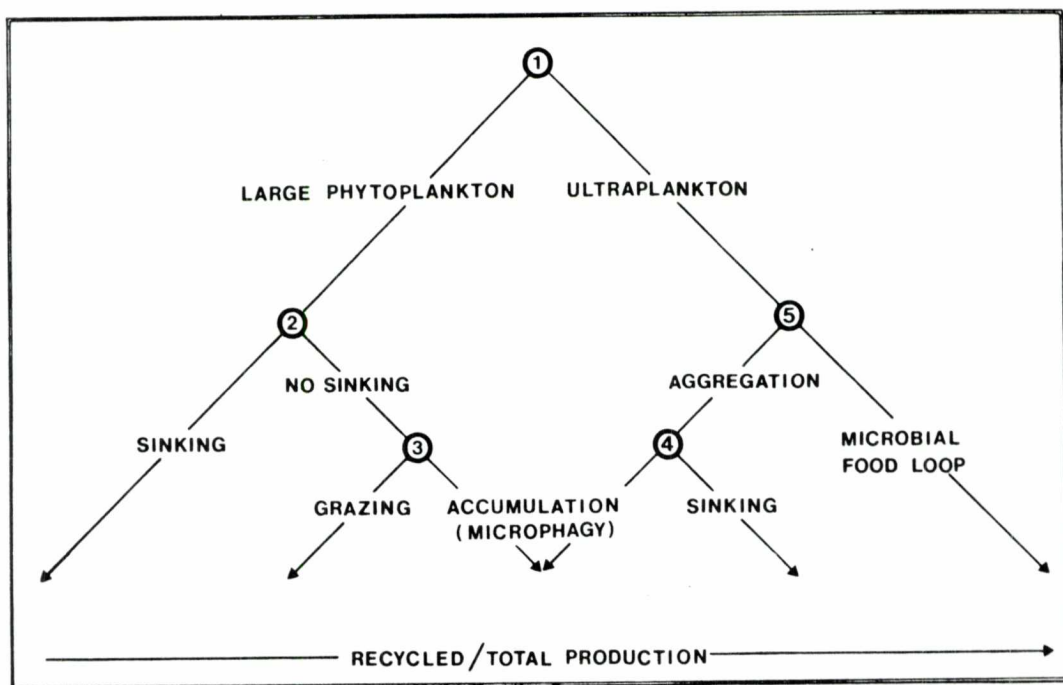


FIGURE 2. Model of export production (downwards arrows) in oceans. At each bifurcation (numbers), part of the production may be channeled into export pathways, which does not preclude coexistence with recycling pathways. The length and complexity on the food webs involved in the export of biogenic carbon increase towards the right. According to Legendre and Le Fèvre (1989), hydrodynamic conditions control the five bifurcations. Reprinted with permission from the Dahlem Workshop Report LS44, p. 51 John Wiley and Sons, Chichester.

Pelagic ecosystems: role in the export and sequestration of biogenic carbon

There are several assumptions underlying the usual steady-state/stoichiometry model of production export in oceans (see the introduction). Legendre and Gosselin (1989) point out that some important fluxes are most often overlooked, such as direct fixation of N_2 gas by microorganisms (case 1, below) and export to depth of refractory dissolved organic matter (case 3). Neglected fluxes also include nitrogen input, in the form of NO_3^- , NH_3 or NH_4^+ , from rainfall and the fallout of atmospheric particles, especially in areas subject to acid rain or industrial contamination. These allochthonous nutrients most likely fuel export of organic carbon to depth. In addition, biogenic carbon fixation is not always proportional to nitrogen assimilation in accordance with the Redfield ratio (case 2). More basically, as stressed by Legendre and Le Fèvre (1992), there exists no physical law of biomass conservation, so that there is no forcing mechanism through which production would directly and automatically be adjusted to new production (and recycled production to regenerated production) over a hypothetical steady-state time scale. Finally, as explained in the Introduction, the model does not consider ecosystems to have a significant influence on the export or sequestration of biogenic carbon (case 4). Contrary to these assumptions, Legendre and Le Fèvre (1991) review four general cases showing that pelagic ecosystems may have a significant effect on the export and sequestration of biogenic carbon in oceans.

Case 1. Direct fixation of N_2 gas by phytoplankton (essentially effected by cyanobacteria) is one mechanism by which marine ecosystems may influence the export of carbon to depth. Until recently, it was assumed that direct fixation of N_2 was negligible in surface waters, because this process does not normally take place in the presence of oxygen. However, recent evidence suggests that the upper layer of

the ocean may offer a variety of reducing environments, potentially favorable for N_2 fixation, and that this process could sometimes occur in the presence of relatively high oxygen concentrations. Production fueled by N_2 fixation should lead to carbon export, and eventual sequestration, in excess of the estimates calculated from the uptake of NO_3^- . This may be especially important in the oligotrophic waters. Out of the pelagic realm, coral reefs may account for a significant share of global N_2 fixation, which is effected by cyanobacteria that form thin films or feltlike mats. Corals also play an important role in carbon sequestration since they precipitate large amounts of dissolved carbonate directly in the euphotic zone (see, under case 2, the discussion on global effects of carbonate precipitation).

Denitrification is the antagonistic process to N_2 fixation, by which oxidized forms of combined nitrogen (NO_3^- , NO_2^- and NO) are reduced to free N_2 gas. As in the case of N_2 fixation, it is generally considered that denitrification only occurs under anaerobic or low-oxygen conditions. In the open ocean, sites favorable for denitrification would be oxygen-deficient portions of the water column, below the euphotic zone. It has been estimated that, over periods of several thousand years, imbalances in which denitrification may exceed N_2 fixation could reduce export production by 20 to 30%, and thus the potential sequestration of carbon.

Case 2. Many plankton organisms export an extra share of carbon, either as organic thecae or in the form of calcareous skeletal structures. Carbon export from ecosystems with such organisms is in stoichiometric imbalance relative to nitrogen, i.e. each atom of nitrogen derived from allochthonous nutrients effectively causes the export of more atoms of carbon than predicted from the Redfield ratio. Many dinoflagellates are enclosed in a theca, usually consisting of cellulose or other carbohydrates. Other organisms synthesize calcareous skeletal structures, including photosynthetic cells (mainly coccolithophores), protozoans (foraminifera) and

metazoans (mainly thecosomatous pteropods). Foraminifera and pteropod tests sink very fast. Coccolithophores are much smaller and should sink individually at a very slow rate; however, since they often are incorporated into the fecal pellets of herbivorous animal (e.g. copepods), their sedimentological behavior may be similar to that of large particles. Calcareous tests may therefore be very efficient in exporting biogenic carbon from the surface, but it must be remembered that these dissolve with depth. In areas deeper than the compensation depth, carbonate-carbon is progressively released into the water column, so that its fate (i.e. rapid release to the atmosphere versus sequestration for tens to hundreds of year in the deep waters) depends on sinking velocity and on the deep circulation. In shallower waters, carbonate sediments may sequester carbon for millions of years (e.g. continental limestone deposits).

Concerning the biogeochemical cycle of carbon, the production of plankton organisms with calcareous tests may lead to rather complex results. Limestone deposits were derived, through biological processes, from atmospheric CO_2 but, at some geological time scales (e.g. glacial/interglacial oscillations), it has been postulated that the precipitation of carbonate by marine organisms may lead to increased atmospheric CO_2 , through changes in the carbonate chemistry of surface waters (i.e. lower alkalinity and concentration of total dissolved CO_2). On the other hand, plankton organisms with calcareous tests generally sink faster than other organic particles produced in surface waters, thus reducing the amount of carbon respired during their downward transit, and the adsorption of organic matter onto calcite particles may contribute to increase the burial of organic carbon in ocean sediments. The production and export of biogenic carbon by calcareous organisms may therefore lead to high sequestration of inorganic and organic carbon, but the overall effect of carbonate precipitation by organisms could, at least on some time scales, be an increase in atmospheric CO_2 .

Case 3. It has been recently proposed that the concentrations of dissolved organic carbon (DOC) and nitrogen (DON) in oceanic waters are much higher than previously thought. Modelling has suggested that about half the new production could be exported to depth as refractory dissolved organic matter (with a characteristic lifetime of 200 years). The partitioning of new production into particulate and dissolved organic matter, under the present conditions of global change, may effectively uncouple the export of biogenic material to depth from the usually measured f -ratio (see the Introduction). However, the refractory DOC could chemically sequester carbon in the surface layer, for periods of interest to global change (i.e. 100s years), before this carbon is transferred by convection into the deep waters, where it is eventually released by respiration. Actual measurements of DOC and DON in marine waters are still controversial, so that the fluxes associated with long-lived organic matter in the oceans are presently poorly known.

Case 4. Hydrodynamic forcing controls production in the oceans through the agency of irradiance and nutrient supply. As explained in the previous section, ecosystems where export production prevails over in situ recycling are most often found in relation with hydrodynamic singularities. In the model of Fig. 2, the production of large cells favors export (left-hand side), while that of small cells results in high recycling (microbial food loop; right-hand side) and corresponding losses of biogenic carbon through respiration.

Conclusion

It follows from the above discussion that a significant component of the biologically driven flux of CO_2 into the oceans is determined from the level of individual cells up (responses to hydrodynamics), and mediated by processes of pelagic ecosystems. The dynamics of marine

ecosystems thus plays an important role in channeling biogenic carbon into export pathways, leading to exploitable living resources or eventual sequestration of carbon. Models for the management of exploited stocks and for predicting the global flux of carbon into the oceans should therefore incorporate relevant characteristics of biogenic particle dynamics and of marine ecosystems.

MICROALGAL BLOOMS AND THE FLUX OF BIOGENIC CARBON IN OCEANS

Types and mechanisms of microalgal blooms

Blooms of marine microalgae provide additional insight into the role of marine pelagic ecosystems with regard to the export of biogenic carbon in oceans. In the euphotic zone, mechanisms responsible for changes in microalgal carbon biomass (B) with time (t) can be summarized as:

$$dB/dt = P - (R + G + S)$$

The various rates (carbon per unit time) on the right-hand side of the equation are: (P) primary production, (R) community respiration, (G) grazing by large herbivores and production of faecal pellets, and (S) sedimentation of intact cells. Microalgal blooms ($dB/dt \gg 0$) result from transient imbalances between P and ($R + G + S$). They are defined by Legendre (1990) as follows: Microalgal blooms are rapid increases in biomass, caused by locally enhanced primary production, that result in abnormally high cell concentrations.

From this definition of blooms, it is possible to draw preliminary conclusions concerning the characteristics of blooming systems. (i) Blooms result from microalgal responses to environmental changes, since they imply enhanced primary production. (ii) Blooms can

develop only when there is an imbalance or a lag between the production of microalgae and their grazing or advection/sedimentation out of the production zone. (iii) In oceans, blooms generally consist of relatively large cells ($> 5 \mu\text{m}$), since small cells ($5 < \mu\text{m}$) are mainly processed by the microbial food loop, from which little material is exported and is therefore in a quasi-steady state. Changes or not in microalgal biomass ($dB/dt > 0$ versus $dB/dt \approx 0$) provide little, if any information on primary production (P) per se, since dB/dt reflects the balance between P and ($R + G + S$). Considering that microalgal blooms ($dB/dt \gg 0$) are unequivocal indications of a transient imbalance between P and ($R + G + S$), Legendre (1990) proposes that the true significance of microalgal blooms mainly concerns the fate of primary production in the marine environment.

Legendre (1990) reviews several types of blooms in oceans, i.e. phytoplankton outbursts primarily governed by irradiance (e.g. spring, ice-edge, under-ice, upwelling and estuarine blooms) or by nutrients (e.g. tidal, summer, episodic and exceptional blooms), and ice-algal blooms. All blooms seem to be controlled by hydrodynamics, through the agency of irradiance or/and nutrient replenishment. The critical depth model (Sverdrup, 1953) accounts for blooms governed by irradiance, and its generalization (Legendre, 1981) to a wide range of temporal scales, including blooms governed by nutrients, shows that enhanced primary production is generally driven by the alternation of vertical destabilization and stabilization of the water column. This generalization is supported by the comprehensive review of Mann and Lazier (1991).

Fate of blooms in oceans and significance for the flux of biogenic carbon

The above discussion indicates that the first condition for a bloom to occur is a physical environment conducive to enhanced primary

production (see the ergocline hypothesis of Legendre *et al.*, 1986). However, a bloom can only develop if primary production is higher than the rate of cell loss from the euphotic zone, caused by microbial consumption and respiration, grazing by large herbivores and sedimentation. (i) Consumption and respiration of autotrophic production by the microbial food web, within the euphotic zone, may sometimes play an important role in the fate of phytoplankton blooms. According to Pomeroy and Wiebe (1988), suppression of the microbial food web at low temperature would explain why regions in the northern hemisphere where the spring bloom occurs between -1.8 and 2°C are also regions with resilient fisheries of consistently high productivity. (ii) Several examples show that large phytoplankton outbursts are not possible when grazing pressure is high. This led Legendre (1990) to conclude that, as general rule, microalgal blooms should develop as an inverse function of grazing pressure. (iii) When in situ recycling and grazing are moderate, one striking outcome of the spring phytoplankton bloom is sometimes massive sinking of intact cells and faecal pellets to the bottom. More transient phytoplankton blooms can also result in significant sedimentation, as is also the case for ice-algal blooms. In summary, microalgal blooms reflect low recycling, and a large degree of uncoupling between increased primary production and grazing by zooplankton. As a consequence, outbursts of microalgae often result in high sedimentation of intact cells and faecal pellets.

In the oceans, there is generally no major imbalance between primary production and its dissipation by grazing (microbial food web and large herbivores) and/or sedimentation of intact cells, i.e. most of the time, microalgal biomass remain in quasi-steady state over most of the ocean. The absence of blooms may be explained by the grazing pressure (i.e. generally $G \approx P$, so that $dB/dt \approx 0$). Fig. 3 schematizes this first case (left-hand side), and also the alternative blooming sequence. Under especial sets of conditions

discussed above, microalgal blooms may develop as transient systems where community respiration, grazing and sedimentation do not balance the enhanced primary production (i.e. $R + G + S \ll P$, so that $dB/dt \gg 0$; Fig. 3, right-hand side). As already stressed, the presence or absence of microalgal blooms provide little, if any information on primary production since enhanced carbon fixation or growth rate do not necessarily lead to a bloom, i.e. $dB/dt \neq P$ except when $(R + G + S)$ are small relative to P . On the other hand, blooming systems ($dB/dt \gg 0$) provide unique information on the potential fate of primary production in marine ecosystems. This is of significance for both fisheries and the export of biogenic particulate matter from the euphotic zone.

Concerning fisheries, most of the energy stored by small primary producers ($< 2\text{-}5\mu\text{m}$) may be dissipated in the microbial food loop before it reaches the larger animals, so that systems dominated by small cells are in quasi-steady state (e.g. oligotrophic waters) and, as a consequence, animals are dispersed. In contrast, systems with high amplitude production cycles (i.e. blooms of $> 2\text{-}5\mu\text{m}$ cells, followed by peak production of herbivores, e.g. subarctic North Atlantic) directly channel primary production through large animals to fish, so that animals tend to be aggregated. According to Cushing (1989), this explains why the great fisheries of the world are based on diatoms and their $> 5\mu\text{m}$ successors in the spring bloom (and, in upwelling areas, the larger flagellates). In systems where there are no major blooms, due to strong grazing of large phytoplankton by herbivores (e.g. Alaskan Gyre in the North Pacific), animals are more dispersed and food chains are often longer. Concerning the export of biogenic particles, it has been explained above how the ratio of recycled to total production increases from left to right in Fig. 2. Blooming systems are at the lower end of the recycled/total production range, and thus provide unequivocal indication of potential export of biogenic particles from the euphotic zone.

A case study using the approach developed above may be found in Legendre et al. (1992b) for the sea-ice related biological production in

polar waters. In ice-covered seas, high algal concentrations (blooms) occur in association with several types of conditions. These blooms

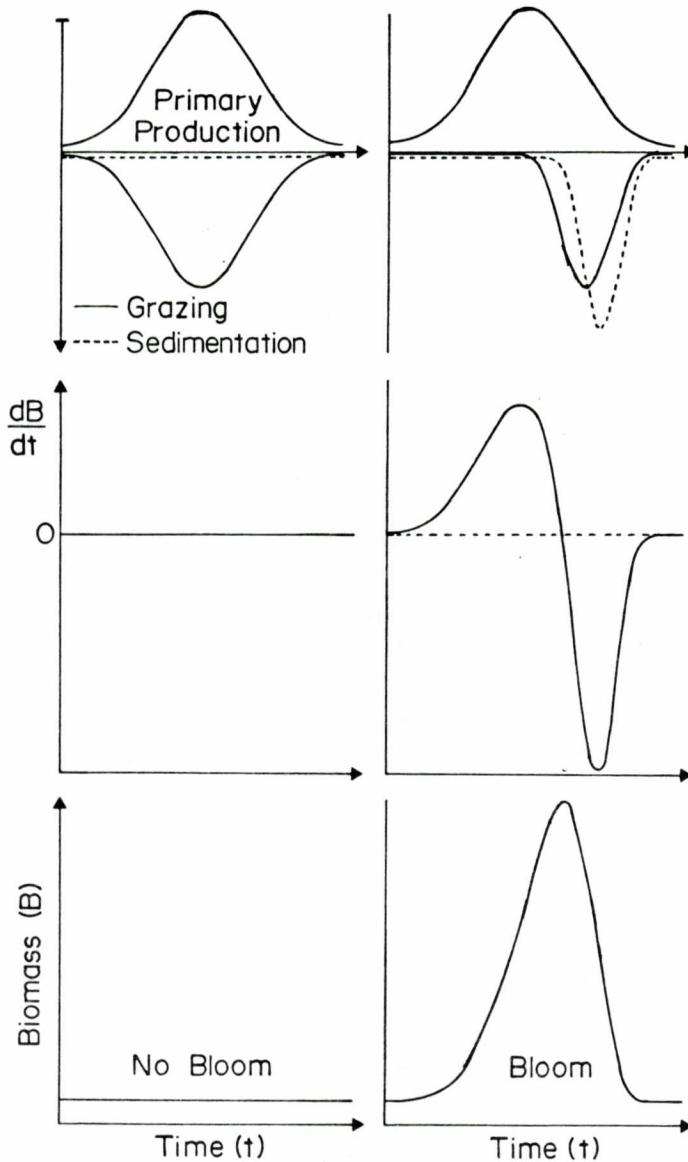


FIGURE 3. Schematic comparison of two marine systems with similar microalgal production, but different grazing and sedimentation rates. Left-hand side: system where zooplankton grazing tracks primary production, so that there is no phytoplankton bloom ($\frac{dB}{dt} \approx 0$). As explained in the text, grazing by microzooplankton or/and large herbivores (e.g. North Pacific Ocean, Norwegian Current) may prevent phytoplankton from blooming. Right-hand side: system where zooplankton grazing lags primary production, which results in a phytoplankton bloom ($\frac{dB}{dt} >> 0$; e.g. spring bloom in the North Atlantic Ocean) and massive sedimentation of intact cells. From Legendre (1990).

often lead to high sedimentation of intact cells and faecal pellets. In addition to ice-related blooms, there is progressive accumulation of organic matter in Arctic multi-year ice, whose fate may potentially be similar to that of blooms. A fraction of the carbon fixed by microalgae that grow in sea ice or in relation to it is exported out of the production zone. This includes particulate material sinking out of the euphotic zone, and also material passed on to the food web. The paper discusses the pathways through which ice algal production does reach various components of the pelagic and benthic food webs, and through them such top predators as marine mammals and birds. Concerning global climate change and biogeochemical fluxes of carbon, not all export pathways from the euphotic zone result in the sequestration of carbon for periods of hundreds of years or more. This is because various processes, that take place in both the ice and the water column, contribute to mineralize organic carbon into CO_2 before it becomes sequestered. In the paper, processes that favour the production and accumulation of biogenic carbon as well as its export to deep waters and sequestration are discussed, together with those that influence mineralization in the upper ice-covered ocean.

Conclusion

Blooming systems provide unique information, of significance for both fisheries and the export of biogenic particulate matter from the euphotic zone. Legendre (1990) concludes that: (i) concerning fisheries, the timing and intensity of microalgal blooms may provide critical information for the management of exploited stocks, and (ii) concerning the study of global fluxes of carbon in the marine environment, first-order estimates of potential export of biogenic particles could be directly

derived from the distribution of blooms over large oceanic areas.

EXPORT AND SEQUESTRATION OF BIOGENIC CARBON IN OCEANS: TYPOLOGY OF MARINE PELAGIC ECOSYSTEMS

Typology of marine pelagic ecosystems

Several authors have pointed out that two contrasting types of ecosystems may be found in temperate and subpolar waters. In both cases, annual and/or maximal levels of carbon fixation by the phytoplankton are relatively similar but, in the first case, there is a well-established spring phytoplankton bloom (e.g. subarctic North Atlantic) while, in the second case, there is little increase in the average seasonal chlorophyll *a* (e.g. Alaskan Gyre in the North Pacific). Parsons and Lalli (1988) explain the observed difference in *standing stocks* by the fact that, in the North Atlantic, there is a lag between phytoplankton production and grazing by zooplankton while, in the North Pacific, both microzooplankton and large-sized copepods react almost immediately to any increase in primary production. As a consequence, *standing stocks* of phytoplankton in the North Pacific are dominated by small cells, while both large and small cells are found in the North Atlantic during the summer, even though the *production* of large and small cells might be similar in the two systems. Such contrasting ecosystems have also been described for other regions, as reported by Legendre and Le Fèvre (1991)

Using the various possible combinations of phytoplankton production and standing stock, as dominated by large or small cells or resulting from a combination of various cell sizes, Legendre and Le Fèvre (1991) designed a typology of marine pelagic ecosystems. Fig. 4 schematizes the five possible patterns linking

TABLE I

| Type | Production | Biomass | Fisheries | Sequestration |
|------|-----------------------|-----------------------|-------------------------|---------------------------|
| 1 | Large cells | Large cells | Sometimes favourable | Mass sinking |
| 2 | Large and small cells | Large cells | Nuisance | Sedimentation & pteropods |
| 3 | Large and small cells | Large and small cells | Favourable: aggregation | High sedimentation |
| 4 | Large and small cells | Small cells | Favourable: dispersion | Respiratory losses |
| 5 | Small cells | Small cells | Not sustained | Respiratory losses |

TABLE I. Five types of marine pelagic ecosystems, as defined by the size distributions of phytoplankton dominating the primary production and the standing stock, respectively (small cells $< 5 \mu\text{m}$; large cells $> 5 \mu\text{m}$). Relevance to fisheries and to the export and potential sequestration of biogenic carbon in oceans. Summarized from Legendre and Le Fèvre (1991).

standing stock to production of phytoplankton. This typology has an operational character, since the production of small versus large cells is under hydrodynamic control (Fig. 2), while the size-distribution of the standing stock is influenced by ecosystem structure, as well as by phytoplankton production. The relationship between the size-distributions of phytoplankton production and standing stock appears to be a fundamental characteristic of the structure of the overall pelagic ecosystem, with consequences for fisheries and for the export and sequestration of biogenic carbon. Table I summarizes the main characteristics of the five types of ecosystems, with regard fisheries and to the export of biogenic carbon in oceans. These are

briefly detailed in the following paragraphs.

Type 1 (production and standing stock dominated by large cells). Large cells, generally consisting of diatoms, are favoured when nutrients are abundant and vertical mixing is strong enough to maintain nonmotile cells in the euphotic zone, while other types of large cells, together with small ones, take over when the environment becomes hydrodynamically less energetic (Margalef, 1978). Primary production dominated by (and thus biomass consisting mainly of) large cells generally corresponds to a diatom bloom, which will occur when a major change in hydrographic conditions (a strong hydrodynamic singularity) suddenly frees the algae from the previously prevailing limitation

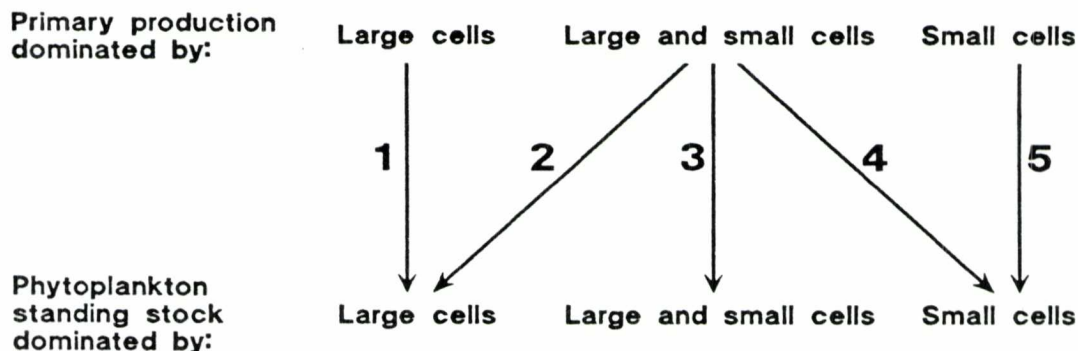


FIGURE 4. Five types of marine pelagic ecosystems, as defined by the size distributions of phytoplankton involved in primary production, on the one hand, and standing stock, on the other hand. Examples of the five types of ecosystems are: (i) upwelling blooms, (ii) exceptional blooms, (iii) the spring bloom in the North Atlantic (iv) the Alaskan Gyre in the North Pacific, and (iv) the oligotrophic ocean. Adapted from Legendre and Le Fèvre (1991).

(as explained in the previous section). Phytoplankton biomass and production dominated by large cells have been reported for various systems, e.g. in upwelling areas and at ice edges. Another case would be the episodic blooms of large cells, hypothesized by Goldman (1988) to occur at the bottom of the euphotic zone in oligotrophic oceanic waters, where short-lived and localized mixing events would allow rapid bursts of growth; these might be responsible for a large fraction of the (new) primary production in deep oceanic waters.

The very development of such diatom blooms implies that no or little grazing is impeding the biomass buildup, a condition that is best met with when no preexisting herbivore stock is ready to take advantage of it, i.e. most often when little primary production was taking place beforehand. Under such circumstances, the most likely fate of the diatoms is their sinking to depth, as documented for receding sea-ice edges

and upwelling areas, and hypothesized for episodic blooms of large cells in open oceanic waters. Rapidly settling cells are efficient in transporting carbon to depths where it may be effectively sequestered.

Type 2 (production by small and large cells, standing stock dominated by large cells). Examples of this type of ecosystem may be the so-called «exceptional» blooms (e.g. red tides and similar phenomena). Some exceptional blooms involve carbon-rich thecate dinoflagellates. Physical conditions leading to exceptional blooms include: for diatoms, strong vertical stratification, low turbidity in vertically mixed waters, wind-induced upwelling, nutrient pulses and eutrophication; for coccolithophores, intermediate turbulence maintained by physical instabilities such as tidal mixing and upwelling; for dinoflagellates, relatively shallow pycnocline/nutricline, controlled by tidal mixing, upwelling or geostrophic effects. Exceptional

blooms often involve phytoplankton species avoided by grazers, or develop in areas where grazing pressure is low. As a result, the biomass of phytoplankton becomes dominated by ungrazed large cells, even in the face of a significant contribution to primary production by small cells.

Effects of exceptional blooms on commercially exploited species include, in the case of toxic species, poisoning and kills of vertebrates (fish, birds and humans) and, more generally, such consequences as mortality resulting from oxygen depletion and mechanical damage to animals (e.g. clogging of fish gills). It appears that there is no case of an exceptional bloom that was of advantage to fishing. Concerning the export of carbon to depth, exceptional blooms can result in significant sedimentation. The ageing standing stock at the final phase of a bloom due to species unpalatable to herbivores is likely to be recycled by decomposers, leading to microphagous metazoans (including carbonate-rich pteropods) under certain conditions. Actual sequestration of carbon would largely depend on the depth of the waters into which the particles will eventually sink.

Type 3 (production and standing stock of small and large cells). This type is exemplified by the annual cycle in the temperate waters of the North Atlantic. Stabilization of the water column in the spring favours a diatom bloom, and more moderate vertical mixing a coccolithophore bloom. In summer, when full stratification has developed, zooplankton biomass has increased and the nutrients are exhausted in the surface mixed layer, primary production is mainly effected by dinoflagellates and smaller flagellates. In places where a seasonal pycnocline develops, a second bloom involving diatoms may occur in autumn. Secondary production of herbivores is dominated by copepods, which overwinter below the euphotic zone at the last copepodite stage and reproduce in spring. For reproducing, the animals require a supply of energy, which is not available before

primary production has begun to take place. A time lag ensues before they can respond to the onset of phytoplankton outgrowth (hence, the spring phytoplankton bloom). A second generation is produced in summer, feeding mainly on regenerated production (i.e. flagellates) before migrating to deep waters for overwintering.

An annual cycle of this type leaves ample room for the export and sequestration of biogenic carbon. As long as the herbivore stock is too low to graze them, the diatoms from the spring bloom will largely sink, as will part of the material from the subsequent coccolithophore bloom. In autumn, recycling of the summer biomass pool by microheterotrophs may result in the buildup of large pteropod populations which will export carbon in their calcareous shells. Similar processes can also take place at other times of the year in hydrodynamic traps, where ageing organisms or detrital material accumulate. Systems with high amplitude production cycles (i.e. blooms of large cells, followed by peak production of herbivores) favour a food web leading to large animals and fish in specific locations where primary production dynamics are tuned to the needs of herbivores. As mentioned in the previous section on blooms, a hydrodynamically structured environment is a major factor in aggregating biomass, in both space and time. This facilitates commercial exploitation. In the case of the North Atlantic, major fisheries are actually found on the continental shelves and slopes on both sides, where the level of hydrodynamic heterogeneity is highest.

Type 4 (production by small and large cells, standing stock dominated by small cells). A good example of this type of ecosystem is found in the Alaskan Gyre of the North Pacific. Little increase in the standing stock of chlorophyll *a* takes place with respect to the winter background level, although the integrated annual production may be similar to that measured in the North Atlantic. At any time, the phytoplankton mainly consists of small flagellates; larger diatoms are

also present, in small numbers, and they eventually dominate samples incubated in the absence of zooplankton. Grazing thus prevents large diatoms from blooming, but large cells effectively contribute to primary production. Production by small cells is normally transferred to microheterotrophs. In the Alaskan Gyre, protozoan standing stocks are eaten by large copepods at the onset of the productive season. These copepods overwinter at the last copepodite stage and reproduce in the spring, at which time they are in good condition; they have a single generation per year, and their reproduction is in phase with the annual increase in primary production. The protozoan biomass may provide an initial food supply, that allows the animals to reproduce at the very beginning of the increase in primary production, and the continuing production is exploited later by their offspring.

In such an ecosystem, where the activities of producers and consumers are largely coupled in time, the export of new primary production will tend to be channeled towards grazing rather than sedimentation. In addition, most of the carbon fixed by phytoplankton may be respired during the long downward transit of the biogenic material, and returned to the atmosphere. This might accordingly result in lower sequestration of carbon than expected from the influx of allochthonous nitrogenous nutrients. Because the environment is rather weakly structured in time and space, the biomass is likely to be dispersed, which can hinder commercial exploitation of the stock.

Type 5 (production and standing stock dominated by small cells). In oligotrophic oceanic waters, picoplankton ($<2\ \mu\text{m}$) typically account for $>50\%$ of the phytoplankton biomass (chlorophyll *a*) and production. The small phototrophic cells are part of the microbial food loop from which, as already explained, little material is exported.

Even if the microbial food web is largely a recycling loop, export of production is nevertheless possible, through direct feeding by

metazoans on small particles, incorporation of small particles into sinking marine snow, and their accumulation with particles of various sizes in hydrodynamic traps where they are subject to grazing by microphagous feeders (see Fig. 2). Actual sequestration of carbon is however subjected to respiratory losses similar to those in Type 4, given the long and inefficient export pathways. Given the fact that the production cycle in the oligotrophic ocean is in quasi-steady state, the food chains are long and the organisms are dispersed. Such conditions do not favour sustained exploitation of fish stocks. Concerning the export and sequestration of carbon, the oligotrophic ocean is probably the system where the assumptions underlying the usual steady-state/stoichiometry model for export production are best approximated. However, even in this case, the task of estimating new production is not trivial (Plat *et al.*, 1989), and the generally accepted mass balance between new and export production is less than certain (Legendre and Gosselin, 1989).

Typology and fate of biogenic carbon in oceans

Legendre and Le Fèvre (1992b) classify the various concepts concerning the export and sequestration of biogenic carbon in oceans by reference to the turnover rate of biogenic carbon, i.e. the time elapsed between the photosynthetic uptake of carbon by phytoplankton and the return of this carbon as CO_2 to surface waters or the atmosphere. They propose to classify biogenic carbon in oceans (Table II), with break points in the continuum of turnover rates at 10^{-2} and 10^2 years. *Short-lived organic carbon* ($< 10^{-2}$ years) does not contribute to building-up the biomass of large animals or sequestering biogenic carbon. It consists of organisms with high turnover rates as well as labile dissolved organic compounds, and it mainly transits through the microbial food web. Renewable marine resources are part of

TABLE II

| < 10 ⁻² years | Turnover time 10 ⁻² to 10 ² years | > 10 ² years | References |
|----------------------------|--|-----------------------------|-------------------------------------|
| Short-lived organic carbon | Long-lived organic carbon | Sequestered biogenic carbon | Legendre and Le Fèvre (1992a) |
| Recycling | Export | Sequestration | Legendre and Le Fèvre. (1989, 1991) |
| Microbial food loop | Traditional food chain | | Cushing. (1989) |
| Regenerated production | New production | | Eppley and Peterson. (1979) |

Table II. Classification of biogenic carbon in oceans, as defined by the turnover time of CO₂ (i.e. the period between the photosynthetic uptake of dissolved inorganic carbon and the return of this carbon as CO₂ in surface waters of the atmosphere), and concepts of biological oceanography usually associated with the three carbon pools. From Legendre and Le Fèvre (1992a).

long-lived organic carbon (10⁻² to 10² years). The biogenic carbon belonging to this pool flows into long-lived animals, and also microbial heterotrophs involved in the breakdown of organic matter derived from large heterotrophs.

Sequestered biogenic carbon (> 10² years) may take various forms, among which organic remains buried in sediments (including oil), inorganic deposits of biological origin (e. g. calcareous, coral reefs, continental limestone), refractory dissolved organic matter, and dissolved CO₂ in deep waters resulting from the oxydation of organic compounds. Climate changes at various time scales, including the possible ongoing global warming, may be related to (or mediated by) variations in the pool of sequestered carbon.

The three pools of biogenic carbon in oceans (Table II) are discussed within the context of the five types of marine pelagic ecosystems (Fig. 4).

(i) The high turnover rate of the microbial food loop (Type 5) results in short-lived organic carbon. In addition, depending on environmental conditions, production of large cells may be either rapidly recycled by the microbial web or channeled toward the other two carbon pools. (ii) Grazing of large phytoplankton by herbivores is the pathway traditionally recognized as leading to large metazoans, and thus long-lived organic carbon. This «traditional food chain» may have different effects on resource exploitation depending on the timing between phytoplankton growth and herbivorous grazing. (i.e. ecosystems of Types 3 versus 4). The «baleen-whale» feeding

of microphagous metazoans on the microbial food web may also influence exploited resources, since appendicularians seem to be a major prey only for flatfish larvae, while larvae of most other fish apparently depend on the traditional food chain. Finally, the ultimate fate of the long-lived organic carbon is oxydation back to CO_2 . As a result of the rapid turnover of carbon in near-surface waters, most of the biogenic carbon exported from the euphotic zone is in fact not sequestered, but rather becomes available for exchange with the atmosphere on time scales of tens of years or less. (iii) The most favourable condition for the sequestration of biogenic carbon is the production of large phytoplankton followed by massive sedimentation of intact cells (blooms in ecosystems of Types 1 and 3). The fate of exceptional blooms (Type 2 ecosystems) is still poorly understood. Another pathway potentially leading to sequestration is the production of fast-sinking faecal pellets by microphagous metazoans feeding on small particles. Sequestration also results from the production of organisms with calcareous test but, as explained above, this may lead to rather complex results concerning carbon flux. Finally, it has already been pointed out that the production of refractory dissolved organic compounds, with a characteristic lifetime of 200 years, could chemically sequester carbon in surface waters, before this carbon is transferred and respired into the deep waters.

According to Legendre and Le Fèvre (1992b), the environmental control of the various pools of biogenic carbon depends on how auxiliary (i.e. mechanical, *sensu* Margalef, 1978) energy is delivered to the pelagic environment. (i) At low levels of auxiliary energy, the hydrodynamic environment is stable and pelagic ecosystems are dominated by the microbial food loop. (ii) Transitions from higher levels of auxiliary energy to more stable conditions favour the production of large phytoplankton. When auxiliary energy is delivered along predictable regular modes, part of the production may be channeled into the long-lived pathway. (iii) In cases where

transitions between the levels of auxiliary energy are stochastic, part of the phytoplankton production may be channeled into sequestered carbon. These ideas are schematized in Fig. 5.

The three pools of biogenic carbon in Fig. 5 are discussed by reference to the control exerted by the environment on the various types of marine pelagic ecosystems (Fig. 4). (i) The microbial food loop dominates environments with low levels of auxiliary energy (Type 5 ecosystems; e.g. the oligotrophic ocean). Under such conditions, most of the biogenic carbon is short-lived, and bacterial activity may rapidly cycle the carbon of not only small but also large particles, depending on water temperature.

(ii) Ecosystems of Types 3 and 4 are generally found in environments with relatively regular cycles of hydrodynamic activity (e.g. seasonal variations). In these ecosystems, organisms such as herbivorous copepods act as a major link, which often favours the channeling of primary production into long-lived organic carbon. This also probably occurs, albeit to a lesser extent, as a result of «baleen-whale» feeding by other metazoans on small particles. Factors responsible for differences between ecosystems of Types 3 and Type 4 are still the subject of an active controversy; concerning hydrodynamics, the difference in the annual cycle of phytoplankton biomass (i.e. occurrence or not of a spring bloom) has been ascribed to the advective nature of Type 3 ecosystems relative to Type 4. (iii) Sequestration of biogenic carbon may be effected through many different pathways, linked to stochastic changes in environmental conditions. There is obviously a variety of cases between the highly stochastic events leading to massive sedimentation of large phytoplankton cells (Type 1 ecosystems) and the more regular environmental sequences where part of the annual primary production by the large cells is channeled into exploited resources (Type 3 ecosystems). Environmental conditions leading to the production of organisms with calcareous structures are, in general, poorly documented, and those favouring the production of refractory

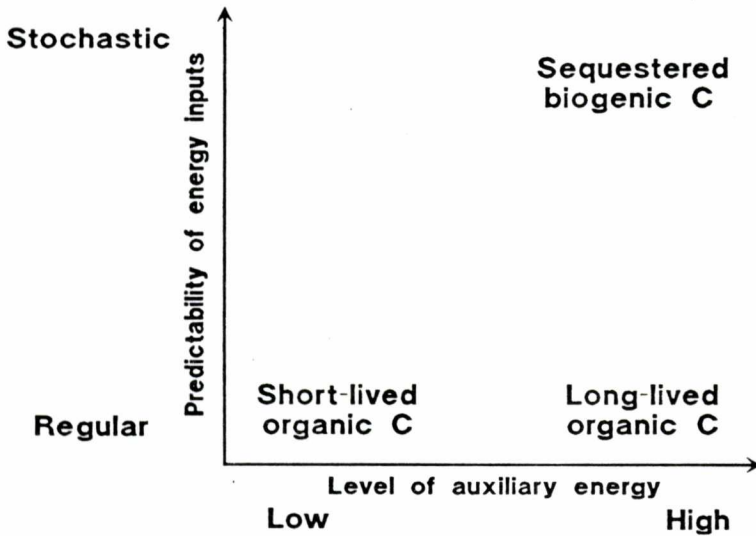


FIGURE 5. Conceptual model relating the three pools of biogenic carbon in oceans (Table 1) to the level of auxiliary (mechanical) energy and the predictability of its delivery into the pelagic environment. Pathways involving microphagous feeders may occupy intermediate situations along the two axes. From Legendre and Le Fèvre (1992a).

dissolved organic compounds are not presently known.

Conclusion

The five types of marine pelagic ecosystems discussed above correspond to different modes of phytoplankton production (as controlled by hydrodynamics) and different structures of the food webs (as reflected in the standing stocks). These influence the pathways of carbon export and sequestration as well as the renewable marine resources. Considering the turnover rate of biogenic carbon in the oceans, it was possible to distinguish between short-lived organic carbon ($< 10^2$ years), long-lived organic carbon (10^2

to 10^2 years) and sequestered biogenic carbon ($> 10^2$ years). Sequestered biogenic carbon is of interest to global climate change, and long-lived organic carbon includes renewable resources; the short-lived component contributes to neither carbon sequestration nor resource exploitation. According to the nature of the interactions between hydrodynamics and ecosystem properties, the photosynthetically fixed carbon may be channeled into either short-lived or long lived-parhways or become sequestered. The fluxes of biogenic carbon in oceans are largely controlled by these interactions, since similar rates of primary production or even export from the surface may result in very different sequestration of carbon, according to the interplay between hydrodynamics and ecosystem processes.

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