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Ocean biogeochemical fluxes: New production and export of organic matter from the upper ocean

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Introduction

Studies of ocean biogeochemical fluxes have been energized in this decade, by the urgency of our need to understand and predict the effects of continued CO_2 accumulation in the atmosphere, by the global perspectives offered by satellite views of ocean color and related physical fields (McClain et al. 1991; Yoder et al. 1992; Mitchell 1994), and by the successful implementation of the Joint Global Ocean Flux Study (JGOFS; Bowles and Livingston, 1993). In this review, I focus on oceanic new production, originally defined as the fraction of primary production supported by inputs of 'new' nitrogen from outside the euphotic zone. With a growing appreciation of the role of this fundamental biogeochemical flux in the global carbon cycle, it has become more common to refer interchangeably to new production so defined, and to the export of organic matter from the upper ocean (e.g.. Sarmiento and Siegenthaler 1992). New production, the driving process of the ocean carbon cycle, is responsible for maintaining over half the vertical gradient in total inorganic carbon. In this review I refer to nitrate-based new production in the open sea, and not to new production supported by other N compounds as observed in the coastal zone. Eppley (1992) gives a personal view of the modern formulation of the concept of equivalence between new production and upper ocean export. This review is dedicated to the memory of John Martin, a friend, colleague, leader and teacher who contributed mightily to our field.

Interdisciplinary Field Programs

Much of the progress in understanding of ocean biogeochemical fluxes has been gained in a series of interdisciplinary field campaigns since the mid-80's. The model for these programs was Vertical Exchange Processes (VERTEX), coordinated by John Martin, and conducted in the north Pacific. Its results are still being published (Harrison et al. 1992). VERTEX was one of the first larger scale programs to focus on the couplings between new production and export, and pioneered the use of surface sediment traps. Other programs with a new production focus included the 1988 WECOMA cruise in the equatorial Pacific (Barber 1992), a predecessor of the JGOFS Equatorial Pacific (EQPAC, Barber et al. 1994) study; Research on Antarctic Coastal Ecosystem Rates (RACER) in the coastal zone of the Antarctic Peninsula (Huntley et al. 1991), the SUPER (Subarctic Pacific Ecosystem Research) program in the north Pacific (Miller et al. 1991; Miller 1993), the 1988 Black Sea Expedition (Murray 1991) and the JGOFS North Atlantic Bloom Experiment (NABE, Ducklow and Harris 1993). Results from the JGOFS time series stations at Bermuda and Hawaii have also begun to appear (Lohrenz et al. 1992; Malone et al. 1993; Roman et al. 1993). The results of these programs will form the basis for the first generation of coupled biogeochemical models now being developed.

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New Primary Production

The global ocean can be divided into three contrasting regions with respect to new production: regions where the stock of surface nitrate is renewed each winter and depleted in the spring by biological utilization; areas where high levels of nitrate persist throughout the year; and large regions in the oligotrophic gyres where nitrate stocks are permanently depleted throughout the euphotic zone. The natural abundance of ^{15}N ($\delta^{15}N$) in core top sediments appears to serve as an indicator of the extent of NO_3 utilization in overlying surface waters (Francois and Altabet 1994), and may help in understanding the history and distribution of the relative strength of the nutrient supply mechanisms vs biological utilization in each province.

NO_3 supplied by deep winter mixing triggers phytoplankton blooms driven by new production in coastal and shelf regions (Townsend et al., 1992; Hansell et al. 1993) including the Southern Ocean (Holm-Hansen and Mitchell 1991; Sullivan et al. 1993), marginal ice zones (Smith 1991) and in the north Atlantic (Campbell and Aarup, 1992; Sambrotto et al. 1993a; Takahashi et al. 1993). Large-scale nutrient fluxes to the north Atlantic supplied by the Gulf Stream (Pelegri and Csanady 1991) drive the basin scale bloom revealed by Coastal Zone Color Scanner imagery. Blooms are characterized by high rates of new production relative to the total production (the f ratio; cf. Garside and Garside 1993), and the uncoupling of production and consumption processes (Karl et al. 1991; Banse 1992; Dam et al. 1993) leading to episodic export of phytoplankton biomass (Honjo and Manganini 1993; Ho and Marra, 1994). Analysis of ocean-wide ratios of nutrient regeneration indicate that organic matter reaching the deep ocean is remineralized in fixed proportions (Anderson and Sarmiento 1994), suggesting that episodic export events might dominate the input of organic matter to the deep sea. This view is not inconsistent with other observations of primary production supported by nutrient utilization at higher C:N ratios (Laws 1991; Banse 1994) and export of dissolved organic matter (see below) if it is assumed that the latter processes do not export new production deeper than about 400 m. During the JGOFS North Atlantic Bloom Experiment, new production was 5-8 mMol N m^{-2} day^{-1} (Bender et al. 1992; Sambrotto et al 1993a) but only a small fraction was recovered in sediment traps (Martin et al. 1993).

Large areas of the ocean in which surface nitrate stays high while phytoplankton stocks are paradoxically low are termed "high-nutrient, low-chlorophyll" or HNLC regions (Cullen 1991). The subarctic north Pacific and central equatorial Pacific are HNLC regions which have been extensively studied in the past decade. Net oxygen production in the mixed layer is becoming a useful and powerful tool for estimating new production, partly because the contributions of physical and biological processes to the O_2 budget can be discriminated with appropriate tracers (Emerson et al. 1991). In the subarctic north Pacific, mass balances of oxygen were used to estimate new production, and compared to estimates from the $^{15}NO_3$ utilization rate , particulate export into shallow sediment traps, and nitrogen mass balance (Emerson et al. 1991, 1993a,b). Different pairs of estimates differed by a factor of two or more. At the current time, this level of uncertainty represents the state of the art in estimating new production and export from the surface layer. In general, new production is low in HNLC regions (Dugdale et al. 1992) but the reasons are still unclear. Intense grazing keeps phytoplankton stocks low (Frost 1991; Frost and Franzen 1992), and ammonium excretion from the grazers inhibits nitrate uptake (Wheeler and Kokkinakis 1990).

In the oligotrophic gyres, there is no measurable NO_3 at depths well below the upper 100 m, and the mechanisms which supply NO_3 to the euphotic zone and maintain new production remain unsolved. The two US JGOFS Time Series stations located in the north Atlantic and Pacific gyres, are addressing this problem. At Bermuda, CO_2 depletion by biological production in spring-summer occurs in the virtual absence of any NO_3, providing another example of non-Redfield production (US JGOFS 1993; Keeling 1993). New production calculated by a variety of approaches including oxygen mass balance (Emerson et al. 1993b), greatly exceeded the annual export caught in sediment traps, suggesting a major uncertainty in our capability to close ocean carbon budgets. In the central north Pacific at the VERTEX time series site (33N, 139W) new production was about 10% of the total annual production and was balanced by export into shallow traps (Harrison et al. 1992). Preliminary results of a mass balance of the oxygen field at the Hawaii station suggest that sediment trap estimates of the particle export do not balance the new production in the euphotic zone above (Emerson et al., 1993b). Thus recent studies in all three 'nitrate provinces' of the global ocean suggest that sediment traps underestimate the export required to balance the estimated new production, or that export by other means than sinking particles must be factored into the balance.

These studies show that new production continues at unequivocally significant rates even in the most oligotrophic regions, in the apparent absence of new NO_3 input from deep mixing. Some other sources have been suggested. Buoyant mats of the diatom *Rhizosolenia* are enriched in NO_3 and might supply 50% of the annual N requirement to the euphotic zone (Villareal et al 1993). Atmospheric input of oxidized and reduced nitrogen species to the global ocean total about. 20×10^{12} gN annually (Duce et al. 1991). This represents 1-2% of the global new production (Table 1), suggesting that aerial deposition is not significant globally. However in nutrient depleted waters of the central gyres, individual deposition events could drive local blooms (Michaels et al., 1993). The air-sea exchange of nitrogen deserves further study, and the balance is not always clear. For example, the sea might be a net source of ammonia to the atmosphere (Zhuang and Huebert 1994). Atmospheric inputs of micronutrients might also stimulate localized episodes of new production in oligotrophic waters (DiTullio and Laws 1991). The major beneficiaries of episodic inputs of new nutrients, whether from above or below, may be large celled diatoms with rapid growth and sinking rates. These cells respond rapidly to nitrogen inputs, even at low light levels, leaving a chemical signature in the form of increased oxygen and dissolved organic carbon (DOC), but sink quickly, leaving little trace of their own biomass (Goldman 1993).

Table 1. Recent Estimates of Oceanic New Production

GtC y^{-1}	Reference
3.4-4.7	Eppley and Peterson, 1979
7.4	Martin et al., 1987
8.4	Bacastow and Meier-Reimer, 1991
10	Sarmiento and Siegenthaler, 1992
12-15	Najjar et al., 1992
8-12	Sarmiento et al., 1993
>15	Sambrotto et al., 1993

The Export Flux

Primary production fueled by new nutrient inputs is balanced over large time and space scales by export of organic matter (both particulate and dissolved; see below) from the upper productive layer into the deep sea. The export flux has been studied principally by sediment traps moored in the deep ocean (Honjo et al. 1992; Jasper and Deuser 1993; Milliman 1993), and also by increasingly numerous deployments of freely drifting traps in the upper 1000 m (Silver and Gowing 1991). Time series observations show that variations in surface productivity are mirrored by fluxes into shallow drifting and deeper moored traps (Altabet et al. 1991; Karl et al. 1991; Asper et al., 1992), suggesting that the traps provide an accurate reflection of the timing of the export process. Comparison of trap collections with camera profiles of large aggregates indicate that fluxes are proportional to large particle concentrations in the water column (Walsh and Gardner 1992).

The accuracy of sediment traps has been questioned, particularly in the upper ocean where biological activity and variability are greatest. At shallower depths in warmer water, bacterial activity must be controlled using poisons to prevent particle decomposition (Lee et al. 1992; Hedges et al. 1993) but poisoning results in accumulation of actively swimming zooplankters ('swimmers') in the traps, leading to overestimates of fluxes. New trap designs appear to segregate the larger swimmers, but small swimmers are not efficiently removed from the passively sinking material (Peterson 1993; Hansell and Newton 1994). Even if the multitude of biological effects can be corrected or prevented, the behavior of traps in moving fluid still needs to be addressed. Traps appear to collect particles in proportion to the particle approach velocities (Gust et al. 1992). The bias will be largest in the upper ocean where velocity shear is greatest.

^{234}Th (Buesseler et al. 1992a) appears to be a powerful tracer of particle flux in the upper ocean. Comparison of observed ^{234}Th fluxes into shallow sediment traps with modeled ^{234}Th removal rates on sinking particles suggests that shallow drifting traps may undercollect or overcollect the particulate flux by factors of 3-10 (Buesseler 1991). ^{234}Th-based estimates of particulate carbon export from ^{234}Th profiles in JGOFS NABE ranged from 5-42% of the primary production (Buesseler et al. 1992b), agreeing with net observed changes in particulate carbon in the upper water column (Bender et al. 1992), but were up to 3 times greater than estimates derived from carbon flux into sediment traps (Martin et al. 1993). The ^{234}Th and ^{228}Th observations in NABE support the idea that microbial activity is responsible for particle aggregation/disaggregation (Cochran et al. 1993).

Transparent exopolymer particles (TEP) of O(100 μm)derived from the extracellular products of bacteria and diatoms harbor bacteria and might constitute sites for particle aggregation and enhanced microbial hydrolytic enzyme activity (Smith et al. 1992; Alldredge et al. 1993). In the subarctic north Pacific (SUPER Program) bacterial production averaged 13% of primary production in the euphotic zone, and bracketed estimates of the particulate organic carbon (POC) flux in the mesopelagic region (100-1000m depths; Simon et al. 1992), suggesting that decomposition of the POC flux supported bacterial metabolism beneath the surface layer. In the Arabian Sea however, even conservative estimates of mesopelagic bacterial production (100 - 1000 m) were in excess of the POC fluxes through the water column, indicating the possible need for an addition source of carbon for the bacteria (Ducklow 1993). Virus activity might play a role in regulating bacterial activity in sinking particles by attacking the particle-associated bacteria and phytoplankton in the vertical flux (Proctor and Fuhrman 1991).

Dissolved Organic Matter

The previously moribund field of DOC analysis was stimulated by recognition that the high surface concentrations of dissolved organic carbon (DOC) reported by Suzuki could form an important component of the export of organic matter from surface waters. Biogeochemical models incorporating DOC as an export term provided improved simulations of nutrient distributions, for example by eliminating the trapping of high phosphate concentrations under the equatorial upwelling (Bacastow and Meier-Reimer 1991; Najjar et al., 1992). These models gave revised global new production estimates of 2.0 - 3.6 Mol C m^{-2} y^{-1} (8-15 GtC y^{-1}) and lent strong support to the observations of a high level of enhanced or 'new' DOC in the surface ocean. In these models about 70-80% of the total export is assigned to the dissolved phase, but it should be noted that this partitioning is defined in the model code rather than being generated by the biogeochemical dynamics of the model itself.

The new interest in DOC by biogeochemists and modelers stimulated a large amount of research directed toward refining and calibrating the high temperature catalytic oxidation (HTCO) technique for analyzing DOC in seawater (Hedges and Farrington 1993). Benner and Strom (1993) showed that assessment of potentially large machine blanks associated with HTCO instruments was necessary for accurate interpretation of analytical data. The original observations of high DOC were withdrawn following interpretation of the blank problem (Suzuki 1993; Hedges et al. 1993). Comparative (Hedges et al. 1993; Sharp et al. 1993) have now demonstrated that the high values were in error and that mean deepwater levels of DOC measured by HTCO techniques are consistent with earlier persulphate and other measurements. However the new techniques have resulted in much improved precision which enables resolution of vertical gradients in the upper ocean (Sharp et al. 1993) as well as of temporal and spatial variability formerly interpretable only as analytical noise.

New analyses of the composition of oceanic dissolved organic matter (DOM) indicate that bulk C:N ratios range from 16-38 (Hansell et al. 1993; Karl et al. 1993). 22-33% of the total DOC is > 1000 molecular weight and composed largely of carbohydrate material, with C:N ratios of 15-22 (Benner et al. 1992). The synthesis of high C:N DOM might be one explanation for observations of non-Redfield utilization of inorganic carbon and nitrogen in both coastal and oceanic regions (Karl et al. 1991; Sambrotto et al. 1993b). Large-celled diatoms continue to fix carbon, in both particulate and dissolved forms following nitrogen depletion (Goldman et al. 1992). The reactive nature of this material suggests that it must play a role in supporting heterotrophic activity, especially bacterial respiration, but utilization is likely to be nitrogen- or phosphorus-limited (Amon and Benner 1994). 20% of the DOC in the surface waters of the north Atlantic during the spring, 1989 phytoplankton bloom was removed by bacteria within 2-3 days (Kirchman et al. 1991). The utilization of the DOC was supported by inorganic nitrogen, suggesting that the biochemically labile fraction was deficient in nitrogen. The processes by which DOC is produced and utilized, and especially those which regulate its escape from complete utilization and subsequent export into the large oceanic DOC reservoir, are just beginning to be understood. Carlson et al. (1994) have showed that DOC export is potentially an important component of the carbon budget at Bermuda. At this point, the relative contributions of DOC and POC to the export of new production are not known within a factor of more than two.

Synthesis and Prospects

Estimates of the total new production are similarly uncertain. It is striking that a synthesis of recent estimates of global annual new production (Table 1) shows an upward trend which has doubled the best estimate in the period covered by this review. This trend parallels the refinement and development of technique, accumulation of data, and deepening of understanding which has occurred over the past few years. The temporal and spatial variability of the ocean is so great as to preclude any reasonable expectation that observations alone will yield accurate global estimates of new production. Large scale syntheses must come from models which build on the results of the process and time series studies reviewed here (Evans and Fasham 1992; Fasham 1993). A coupled model of the physical, biological and nutrient fields observed in the 1989 JGOFS NABE assimilated satellite altimetric estimates of sea surface height to demonstrates the vital role of eddy circulation in driving new production (Robinson et al. 1993). Future models will assimilate ocean color observations. The first coupled basin scale models of ocean circulation and biogeochemistry which describe biogeochemical processes including new production explicitly have only been developed in the past 5 years (Fasham et al. 1993; Sarmiento et al. 1993). Their model has a simple generic ecosystem structure which nonetheless has over 20 parameters to be evaluated. A scheme based on the allometric scaling of biological parameters may simplify the parameter evaluation process (Moloney and Field 1991). Inverse techniques borrowed from geophysics are now routinely applied to the analysis of biogeochemical systems to recover unmeasured or poorly estimated rates processes (e.g. new production, export, grazing) from observed data (Jackson and Eldridge 1992). The next generation of biogeochemical flux studies must combine new observational and modeling approaches to gain the factor of 2 or greater improvements in precision required to constrain the global carbon budget.

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