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Influence of mesoscale eddies on new production in the Sargasso Sea

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It is problematic that geochemical estimates of new production—that fraction of total primary production in surface waters fuelled by externally supplied nutrients—in oligotrophic waters of the open ocean surpass that which can be sustained by the traditionally accepted mechanisms of nutrient supply.^{1,2} In the case of the Sargasso Sea, for example, these mechanisms account for less than half of the annual nutrient requirement indicated by new production estimates based on three independent transient-tracer tech-

niques^{2–6}. Specifically, approximately one-quarter to one-third of the annual nutrient requirement can be supplied by entrainment into the mixed layer during wintertime convection⁷, with minor contributions from mixing in the thermocline^{8,9} and wind-driven transport¹⁰ (the potentially important role of nitrogen fixation¹¹—for which estimates vary by an order of magnitude in this region¹²—is excluded from this budget). Here we present four lines of evidence—eddy-resolving model simulations, high-resolution observations from moored instrumentation, ship-board surveys and satellite data—which suggest that the vertical flux of nutrients induced by the dynamics of mesoscale eddies is sufficient to balance the nutrient budget in the Sargasso Sea.

The notion that mesoscale (of the order of 10² km) processes could be an important vehicle for nutrient transport has been debated for some time^{13,14}. Analysis of an apparently eddy-driven event observed at Station S near Bermuda in 1986 suggested that only a few such events per year would be required to account for the total new production¹⁵. A variety of mechanisms have been proposed as causes of vertical nutrient flux, from the spindown of anticyclonic vortices¹⁶ to submesoscale upwelling patches in meandering jets^{13,17}. Modelling studies in the northeast Atlantic Ocean^{18,19} suggested substantial nutrient fluxes associated with cyclonic eddies and their interactions with adjacent features. Recent work²⁰ has indicated that mesoscale eddies could be the dominant mode of nutrient transport in the open ocean.

Using a regional eddy-resolving model, McGillicuddy and Robinson²⁰ constructed long-term aseasonal simulations characteristic of the mesoscale environment in the Sargasso Sea. Detailed comparisons with observations (eddy kinetic energies, space and time scales) demonstrate that the simulations contain statistically realistic representations of mesoscale fluctuations. Incorporation of a simplified biological model into these calculations facilitated study of the mechanisms by which eddy processes can transport nutrients into the euphotic zone. Results show²⁰ that upwelling due to the formation of cyclonic eddies and subsequent intensification caused by interaction with surrounding features cause sporadic nutrient injections into the surface layer. These calculations indicate the annual flux resulting from the eddy upwelling process in the

Table 1 Geochemical estimates of new production in the Sargasso Sea and nitrate sources

Method		Value (mol N m ⁻² yr ⁻¹)	Reference
O ₂ utilization		0.48 ± 0.10	Ref. 5
		0.42 ± 0.09	Ref. 2
O ₂ production		0.46 ± 0.09	Ref. 2
		0.39 ± 0.16	Ref. 3
		0.51 ± 0.14	Ref. 3
³ He flux gauge		0.56 ± 0.16	Ref. 6
		0.47 ± 0.15	W. J. Jenkins, personal communication
		0.70 ± 0.20	Ref. 27
Nitrogen demand		0.50 ± 0.14	

Nitrate sources			
Process	Method	Value (mol N m ⁻² yr ⁻¹)	Reference
Wintertime convection	O ₂ production	0.17 ± 0.05	Ref. 7
	NO ₃ removal	0.09 ± 0.04	Ref. 7
Diapycnal diffusion	Microstructure	0.05 ± 0.01	Ref. 8
Ekman flow	Climatological hydrography and winds	0.03 ± 0.01	Ref. 10
Eddy upwelling	Simulation	0.35 ± 0.10	Ref. 20
	Satellite-based statistical model	0.19 ± 0.10	This work
	Nitrate supply	0.48 ± 0.17*	

* Excludes nitrogen fixation, for which estimates are very poorly constrained (ranging from 0.05 to 1.3 mol N m⁻² yr⁻¹ in the Sargasso Sea²⁸).

Sargasso Sea is $0.35 \pm 0.1 \text{ mol N m}^{-2} \text{ yr}^{-1}$, which is sufficient to reconcile the apparent discrepancy in the nutrient budget described above (Table 1).

We consider the following conceptual model of the eddy upwelling mechanism (Fig. 1). A density surface of mean depth Z_0 is coincident with the depth of the euphotic zone. This density surface is perturbed by the formation, evolution and destruction of meso-scale features. Nutrients injected into the euphotic zone by shoaling density surfaces are fixed by the biota, whereas deepening density surfaces serve to push nutrient-depleted water out of the well-lit surface layers. The asymmetry imposed by the light field thus rectifies vertical displacements (both up and down) into a net upward transport of nutrients.

Recent advances in the theory of advective effects on planktonic ecosystems provide a context in which to examine analytically the biological response to injection events²¹. Arrival of nutrients to a particular depth in the light-saturated layer stimulates phytoplankton growth which is at first linear. Nutrients begin to accumulate and then decrease rapidly as the phytoplankton population enters a phase of exponential growth. Using parameters relevant to the Sargasso Sea, the response time is one to several days. These findings are in line with earlier work demonstrating biological capability for rapid utilization of episodic nutrient inputs²², and are consistent with the fact that near-surface nitrate concentrations in this region remain below the limit of detection except during periods of wintertime convection.

Given that the eddy driven nutrient flux is such a large component of the annual budget, it is surprising that this mechanism could function largely undetected by biweekly to monthly discrete water sampling in shipboard time-series operations off Bermuda. Monthly observations tend to undersample this highly sporadic process²⁰. Furthermore, the time required for biological removal of new nutrient is much quicker (days) than that of the supply mechanism (weeks). This dichotomy in timescales makes it very difficult to observe evidence of a nutrient injection directly with traditional shipboard hydrographic methods.

High-resolution time series using moored instrumentation provides an observational approach capable of resolving these intermittent events. The Bermuda Testbed Mooring has been deployed since June 1994 ~80 km southeast of that island, near the Bermuda Atlantic Time Series (BATS) site²³. During the summer of 1995, an eddy event was observed (Fig. 2). Dramatic cooling began on day 185 of the year and persisted for 30 days. The record from an automated nitrate analyser²⁴ placed near the base of the euphotic

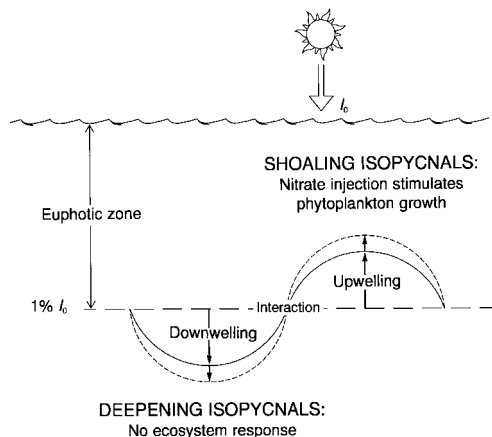


Figure 1 A schematic representation of the eddy upwelling mechanism. The solid line depicts the vertical deflection of an individual isopycnal caused by the presence of two adjacent eddies of opposite sign. The dashed line indicates how the isopycnal might be subsequently perturbed by interaction of the two eddies. I_0 represents incident solar radiation, and $1\% I_0$ the base of the euphotic zone.

zone showed nutrient enhancement associated with this event, in which nitrate concentrations rose from undetectable to 1.4 mmol m^{-3} . This was accompanied by increases in both chlorophyll fluorescence and beam attenuation coefficient, indicating high concentrations of both phytoplankton biomass and particulate material. Chlorophyll during this period was apparently the highest observed in the BATS program to date.

The magnitude and duration of these temporal changes in physical and biogeochemical properties is consistent with the eddy upwelling mechanism described above. The eulerian timescale for the passage of such features can be calculated by dividing a typical eddy diameter (~150 km) by a characteristic propagation speed (~5 km d⁻¹; ref. 25) which yields an estimate of one month (precisely that of the observed event). The magnitude of the temperature decrease and associated nitrate enhancement at the base of the euphotic zone are consistent with an isopycnal displacement of ~80 m. Assuming complete nitrate utilization, only four events of this size are needed each year to provide the annual budget.

Monthly sampling during time-series operations at the BATS site is also supplemented by periodic 'validation' cruises which are used to provide spatial context for the fixed-point observations. One such survey was conducted in June 1996 (Fig. 3). The hydrographic structure included two cold features in the northwestern and eastern portions of the domain, and a warm anomaly to the south. These structures had a dramatic influence on the nitrate distribution just below the euphotic zone. Nitrate concentrations were below the limit of detection in the core of the warm feature, and in excess of 2 mmol m^{-3} in the interiors of the two cold anomalies. Phytoplankton biomass patterns (indicated by chlorophyll) within the euphotic zone corresponded to the underlying nitrate distribution. Although

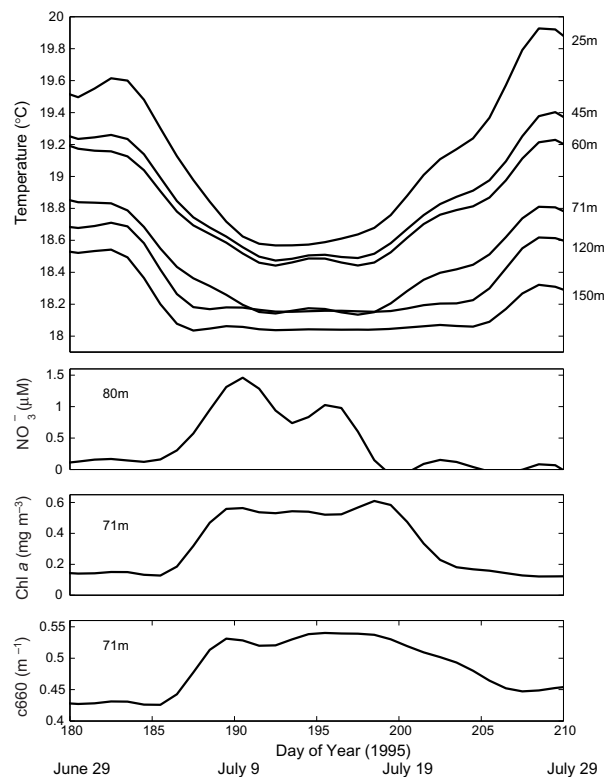


Figure 2 Results from Bermuda Testbed Mooring deployment 3 during the summer of 1995. Upper panel, temperature records at various depths; lower three panels, nitrate concentration at 80 m, chlorophyll fluorescence and beam attenuation coefficient (c660) at 71 m. All signals have been filtered via a six-day moving average. Chlorophyll values of the broadband data exceed 1.4 mg m^{-3} .

the correlation is not exact, biomass is generally lower above the warmer nutrient-depleted waters, and higher above colder more nutrient-rich areas.

Given the conceptual model of the eddy upwelling mechanism, it is possible to estimate nutrient fluxes based on altimetric determinations of the eddy field. Dynamical and empirical mode analyses demonstrate that the vertical structure of these eddy signals are dominated by the first baroclinic mode²⁵, enabling the use of satellite-derived sea-level anomaly (SLA) data to infer sub-surface isopycnal displacements. At the BATS site, isopycnal displacements at 300 m depth are correlated with Topex/Poseidon SLA ($r^2 = 0.62$) with a slope of 4 m of isopycnal displacement per 1 cm of SLA. Using

this information and the mean relationship between density and nitrate concentration derived from BATS data, the upward flux of nitrate across the base of the euphotic zone is estimated to be $0.19 \pm 0.1 \text{ mol N m}^{-2} \text{ yr}^{-1}$ (Table 1). This estimate is roughly consistent with, although smaller than, the results obtained by McGillicuddy and Robinson²⁰.

Although this empirically derived relationship between SLA and isopycnal displacement at the base of the euphotic zone is statistically significant, this simple model cannot accurately represent the complex vertical structure which is sometimes observed. In fact, analysis of the hydrographic time series bracketing the mooring record described above reveals that the doming of the seasonal thermocline (which resulted in the nitrate pulse and exceptionally high chlorophyll) was accompanied by a depression of the main thermocline. The net effect results in a positive SLA, as opposed to the negative signature characteristic of cyclones. Thus, nitrate flux associated with features of this type is not accounted for in this approach. However, similar vertical structures have been observed only four times in the nine-year BATS hydrographic record (although sampling remains an issue). Nevertheless, this statistical model should underestimate new production. Further synthesis of *in situ* observations with remote sensing in the context of data-assimilative dynamical models offers an opportunity to better understand the role of intermittent processes in biogeochemical cycling in the ocean.

We point out that the mechanism presented here cannot account for the summertime drawdown of dissolved inorganic carbon observed at BATS. Eddy induced upwelling of nitrate will be accompanied by a commensurate flux of dissolved inorganic carbon in Redfield proportion. The findings reported here therefore tend to exacerbate previously described problems in balancing carbon budgets in the Sargasso Sea²⁶. □

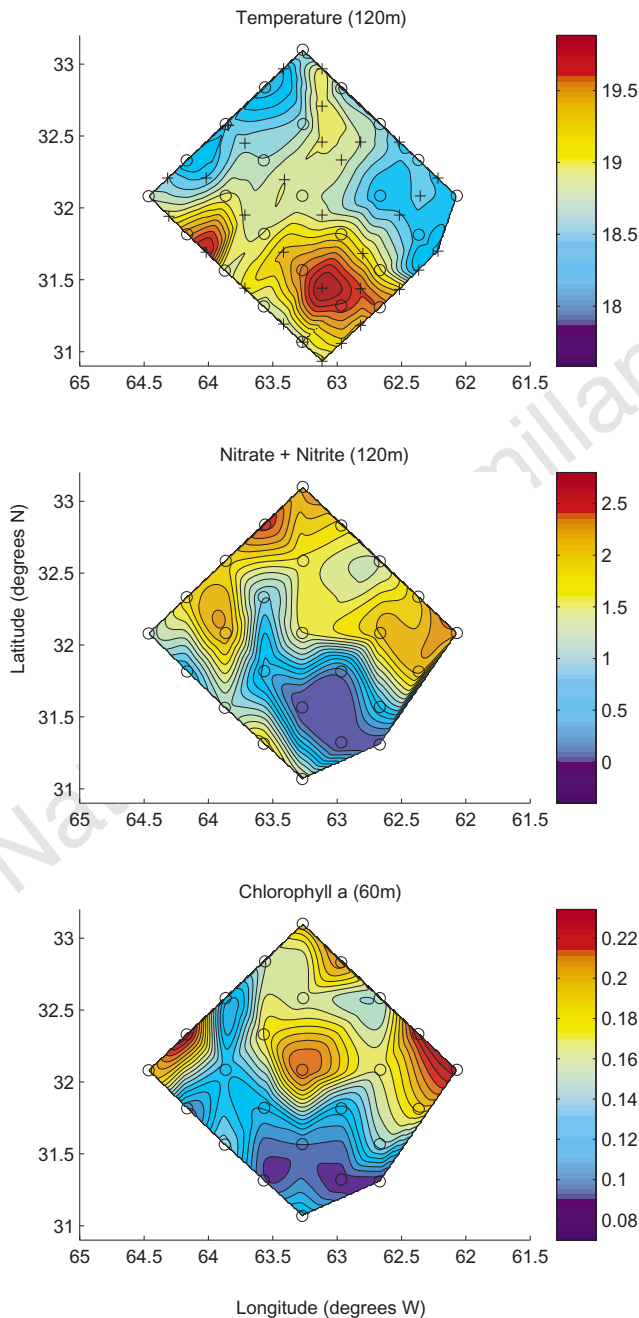


Figure 3 Results from a mesoscale biogeochemical survey near the BATS site occupied from 24 to 28 June 1996. Top, temperature at 120 m (°C); middle, nitrate + nitrite at 120 m (mmol m⁻³); bottom, chlorophyll *a* at 60 m (mg m⁻³). Circles and crosses indicate hydrographic stations and expendable bathythermograph casts, respectively.

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Eddy-induced enhancement of primary production in a model of the North Atlantic Ocean

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In steady state, the export of photosynthetically fixed organic matter to the deep ocean has to be balanced by an upward flux of nutrients into the euphotic zone¹. Indirect geochemical estimates² of the nutrient supply to surface waters have been substantially higher than direct biological and physical measurements³, particularly in subtropical regions. A possible explanation for the apparent discrepancy is that the sampling strategy of the direct measurements has under-represented episodic nutrient injections forced by mesoscale eddy dynamics, whereas geochemical tracer budgets integrate fluxes over longer time and space scales. Here we investigate the eddy-induced nutrient supply by combining two methods potentially capable of delivering synoptic descriptions of the ocean's state on a basin scale. Remotely sensed sea-surface height data from the simultaneous TOPEX/Poseidon and ERS-1 satellite missions are assimilated into a numerical eddy-resolving coupled ecosystem–circulation model of the North Atlantic Ocean. Our results indicate that mesoscale eddy activity accounts for about one-third of the total flux of nitrate into the euphotic zone (taken to represent new production) in the subtropics and at mid-latitudes. This contribution is not sufficient to maintain the observed primary production in parts of the subtropical gyre, where alternative routes of nitrogen supply will have to be considered.

Assuming that nitrogen is the nutrient limiting biological production in the well-lit upper ocean, all primary production associated with the newly available nitrogen is called new production⁴. Geochemical estimates of space- and time-averaged new production, based on oxygen production and consumption or using tritiogenic ^3He as a flux gauge², have been significantly higher than local and instantaneous measurements of nitrate uptake in incubation experiments, which in turn were consistent with turbulent flux estimates based on microstructure measurements³. Intermittent nutrient pulses by eddy-induced upwelling have been suggested to resolve the observational discrepancy. There is evidence both from observations⁵ and idealized model studies^{6,7} that cyclonic flow anomalies, by raising isopycnal surfaces, can lead to local upwelling of nutrient-rich water into the euphotic zone. Eddies might also enhance the lateral transfer of nutrients from the nutrient-rich regions surrounding the subtropical gyre⁸.

To investigate the influence of mesoscale eddies on biological

production in a realistic environment on a basin scale, a four-component pelagic ecosystem model is coupled to a $(1/3)^\circ$ resolution model of the North Atlantic circulation⁹ derived from the WOCE Community Modeling Effort¹⁰. The numerical model has 37 levels in the vertical, with a grid spacing increasing from 11 m at the surface to 250 m at depth. It is forced with monthly climatological data sets, and lateral boundaries are closed with buffer zones at which temperature and salinity are relaxed to observed climatological values¹¹. In order to better represent the mixed-layer dynamics, a turbulent kinetic energy closure scheme has been implemented¹². Optical properties of the water column are modelled by an analytical formula¹³ for clear ocean water plus a simple exponential absorption law taking into account phytoplankton self-shading.

The model framework for the plankton dynamics is a classical N-P-Z-D (nitrate, phytoplankton, zooplankton, detritus) nitrogen-based biological model. Processes within the trophic chain include phytoplankton growth and mortality, zooplankton growth by grazing

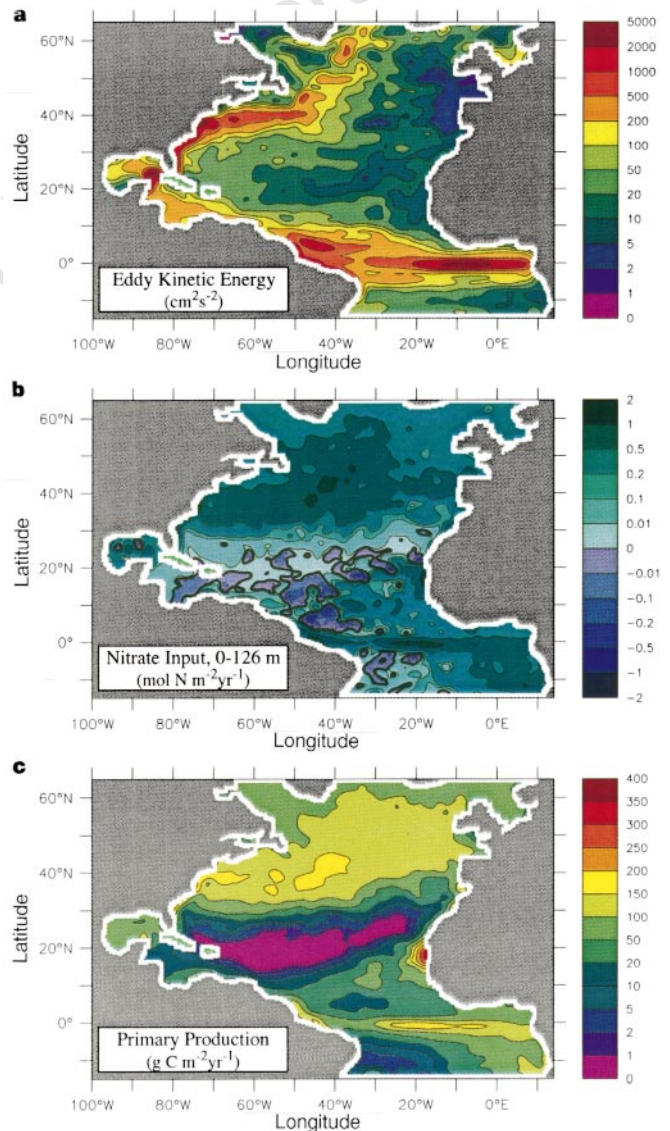


Figure 1 Results from the assimilation experiment A. **a**, Surface eddy kinetic energy (EKE), which contains all deviations from the annual mean, computed for a depth of 60 m to avoid contamination by shallow Ekman currents (in cm^2s^{-2}). **b**, Annual mean nitrate flux into the upper 126 m, which is taken as proxy for the euphotic zone (in $\text{mol N m}^{-2}\text{yr}^{-1}$). **c**, Annual mean primary production (in $\text{g C m}^{-2}\text{yr}^{-1}$). A constant ratio of C:N=6.6 was assumed to give carbon fluxes from the model. This is a rather conservative assumption²⁷ and will give minimal estimates of carbon fluxes.