The role of mesoscale variability on plankton dynamics in the North Atlantic

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Abstract

The intensive field observational phase of JGOFS in the North Atlantic Ocean has shown the importance of oceanic mesoscale variability on biogeochemical cycles and on the strength of the ocean biological pump. Mesoscale physical dynamics govern the major time/space scales of bulk biological variability (biomass, production and export). Mesoscale eddies seem to have a strong impact on the ecosystem structure and functioning, but observational evidence is rather limited.

For the signature of the mesoscale features to exist in the ecosystem, the comparison of temporal scales of formation and evolution of mesoscale features and reaction of the ecosystem is a key factor. Biological patterns are driven by active changes in biological source and sink terms rather than simply by passive turbulent mixing. A first modelling assessment of the regional balances between horizontal and vertical eddy-induced nutrient supplies in the euphotic zone shows that the horizontal transport predominates over the vertical route in the subtropical gyre, whereas the reverse holds true for the other biogeochemical provinces of the North Atlantic. Presently, despite some difference in numbers, the net impact of modelled eddies yields an enhancement of the biological productivity in most provinces of the North Atlantic Ocean.

Key issues remaining include variation on the mesoscale of subsurface particle and dissolved organic matter remineralization, improved knowledge of the ecological response to patterns of variability, synopticity in mesoscale surveys along with refining measures of biogeochemical time/space variability.

Eventual success of assimilation of in situ and satellite data, still in its infancy in coupled physical/biogeochemical models, will be crucial to achieve JGOFS synthesis in answering which data are most informative, standing stocks or rates, and which ones are relevant. Depending on which end of the spectrum quantification of the effect of mesoscale features on production and community structure is required, complementary strategies are offered. Either one may choose to increase resolution of models up to the very

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fine mesoscale features scale (a few kms) for the high end, or to include a parametric representation of eddies for the low end. © 2001 Elsevier Science Ltd. All rights reserved.

1. Introduction

Large-scale ocean circulation is governed almost everywhere by a broad spectrum of intense low-frequency fluctuations. In many regions, the mesoscale part of the frequency-wavenumber spectrum of ocean kinetic energy, roughly corresponding to time-scales between 20 and 150 days and spatial scales from 10 to 500 km, exhibits a particular concentration of energy (Le Traon et al., 1990; Le Traon, 1991). Synoptic maps of oceanic state variables are generally dominated by current meanders and mesoscale eddies, much like weather maps in the atmosphere. Current meter data from moorings are almost always dominated by current fluctuations, and even multi-year time series do not necessarily allow the determination of a statistically significant mean flow (Zenk and Muller, 1988). Eddies transport heat, momentum, physical and biogeochemical water properties and interact with the mean flow field via Reynold stresses. How to measure and quantify the role of the mesoscale variability on the biology of pelagic ecosystems constitutes a formidable challenge. The spatial and temporal intermittency of the eddy variability poses a difficult sampling problem. Proper resolution will require a time series of synoptic three-dimensional physical and biogeochemical measurements. A remarkable number of advances in multi-disciplinary in situ instrumentation has enabled oceanographers to expand the temporal and spatial scale of biological measurements on scales comparable to those of physical measurements (Dickey, 1988). However, the issue of synopticity of hydrographic surveys is a crucial one. Indeed, Allen et al. (2000) show that significant errors in the accuracy of vertical velocities, diagnosed from the geostrophic field and suitable boundary conditions, arise from the necessary compromise between spatial resolution and synopticity of a hydrographic survey. Using both a numerical and an analytical models, they can analyze components of these errors and indicate key parameters for the design of mesoscale sampling. The advent of remote sensors and availability of satellite imagery was the key step to thoroughly appreciate the degree of mesoscale oceanic variability. Remote sensing has immensely contributed to our ability to obtain physical and biological information at comparable temporal and spatial scales.

The strongly nonlinear dynamics of oceanic foodwebs are determined by both the distribution and movement of populations of organisms (which are highly influenced by the physical structures and motions in the ocean), and their growth, death, metabolism, predator–prey interactions, and other behavorial traits. These biological factors vary in time and space in complex, and at present, largely unknown ways. For the mesoscale physical variability to strongly impact ocean biology/biogeochemistry, the physical and biological time-scales (typically, but not necessarily phytoplankton growth rates) must be comparable.

Mesoscale physical phenomena interact with upper ocean biogeochemistry through horizontal advection (Williams and Follows, 1998) and lateral stirring of water masses, frontal instabilities inducing tilting of isopycnal surfaces that enable vertical transport by isopycnal advection and mixing (Jenkins, 1980; Woods, 1988; Onken, 1992) and the eddy pumping mechanism in which the formation and intensification of cyclonic eddies uplift nutrient-replete, isopycnal surfaces into the euphotic zone (Jenkins, 1988a,b; Falkowski et al., 1991; McGillicuddy and Robinson, 1997). Fronts

and eddies are closely related. Unstable fronts develop ageostrophic circulation that may upwell ribbons of high-nutrient water along the front, subduct chlorophyll-rich features or spin-off nutrient-rich eddies (Martin et al., 2000). In addition to interacting with each other to form fronts, eddies can produce significant vertical transport through a variety of internal and external mechanisms (McGillicuddy et al., 1995; Spall and Richards, 2000a).

JGOFS, after completion of its intensive field observational phase, has entered its synthesis phase (Hanson et al., 2000). In the North Atlantic ocean, most of the effort has been spent on local studies, sampling individual sites either intensively, for a limited period, such as the 1989 North Atlantic Bloom Experiment (NABE; Ducklow and Harris, 1993) or the EUMELI experiment (Morel, 2000), or at regular intervals for many years, such as the Bermuda Atlantic Time Series Study (BATS; Michaels and Knap, 1996). These local studies span different biogeochemical provinces (Longhurst, 1995) as well as different mesoscale variability regimes. This paper aims towards answering the overarching question: How does mesoscale variability impact the large-scale patterns and magnitudes of biogeochemical fluxes in the North Atlantic ocean? More specifically we will address the current state of the field, focusing on (i) What have we learned? (ii) What are the key unknowns? (iii) How can we make significant progress? Section 2 will be devoted to a brief description of the eddy field in the North Atlantic. In Section 3, we will highlight the importance of mesoscale variability on remotely sensed data and JGOFS field data acquired in the North Atlantic Ocean. In Section 4, we will show how process, regional and basin-scale models have contributed to enhance, our understanding of the underlying mechanisms. These sections have no pretensions to be all encompassing, rather they will survey these aspects focusing on the three questions mentioned above. The domain that will be covered includes the western subtropical gyral province bounded to the west by the eddy field of the Gulf Stream (of significant mesoscale hydrodynamic variability), the intermediate mesoscale variability regions such as the North Atlantic drift region and the eastern subtropical gyral province, and the weakest variability province, the tropical gyral province. We then try to put together results into a connected whole to start resolving the issue of quantification of the eddy variability on the biogeochemical cycles.

2. Characterization of the physical eddy environment

Oceanic mesoscale variability can be summarized as the result of (i) the direct response to local and/or remote high-frequency surface forcing by the wind and buoyancy effects, (ii) dynamical instability process, including barotropic and baroclinic instability of the mean flow, (iii) eddy generation by flow over and around topography, and (iv) stable baroclinic Rossby waves.

Recent improvements in satellite altimetry and of high-resolution numerical models of the ocean have led to new insights into the nature of the ocean mesoscale in terms of the regional dependence of amplitude and spectral characteristics. Both fields indicate a close association of the observed eddy kinetic energy distributions with the (local) mean baroclinic flow (Beckmann et al., 1994; Stammer and Boning, 1996; Stammer, 1998). Eddy scales associated with observed open-ocean mesoscale features are strongly correlated with the first-mode Rossby radius of deformation (the natural horizontal response scale when both rotation and stratification effects are significant; Pedlosky, 1987). All this is consistent with the hypothesis that mean flow instabilities are the major source of eddy energy over most of the areas of the mid-latitude oceans.
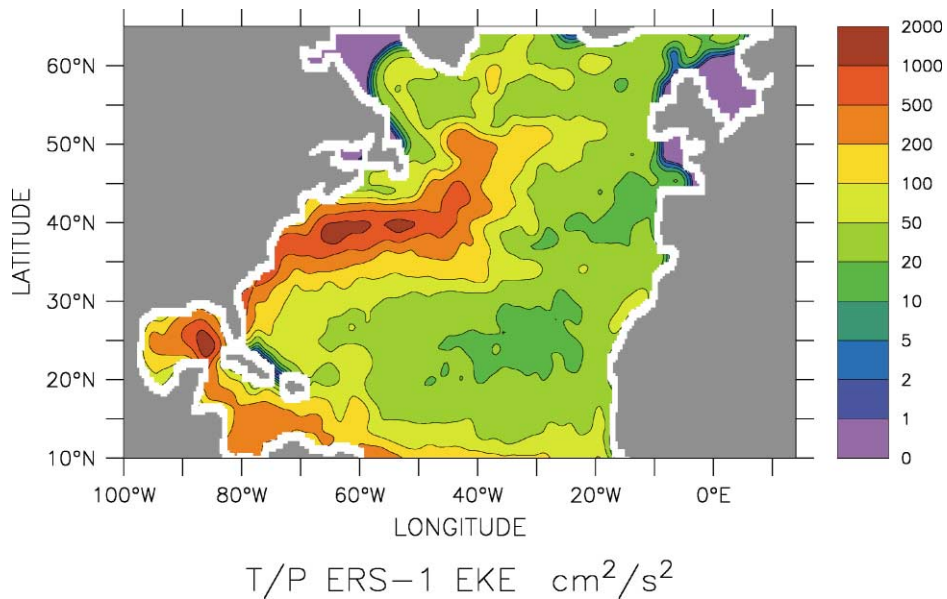
Fig. 1. Surface eddy kinetic energy (EKE, in cm^2/s^2) for a 1-year (October 1992 until October 1993) combined TOPEX/POSEIDON-ERS-1 altimeter data. Observed EKE values have been obtained using geostrophic surface velocities derived from five daily maps of sea-surface height (Oschlies and Garçon, 1998).

The eddy kinetic energy in the North Atlantic ocean inferred from 1 year of combined TOPEX/POSEIDON (henceforth T/P) and ERS-1 sea-surface height fluctuations (Fig. 1), or from 4 years of T/P altimetric data (Stammer and Wunsch, 1999), shows a pronounced inhomogeneity in its geographical distribution. Maxima in eddy kinetic energy are found along boundary currents, but bands of higher energy extend into the interior along the mean positions of the major frontal structures and current systems such as the North Atlantic Current and the Azores Front. Minimum variability (with surface eddy kinetic energy less than $20 \, cm^2/s^2$) is found at mid-latitudes between $37°$ and $47°$N east of $30°$W, and in the central subtropical gyre east of $50°$W, between $20°$ and $30°$ N, south of which values increase equatorward (Stammer and Boning, 1996). Characteristic time-scales estimated from the autocovariance function of sea-surface height vary latitudinally, of roughly 20–30 days in the tropics and mid-latitudes decreasing to 10–15 days in the subpolar North Atlantic (Stammer, 1997). Eddy length-scales, using the integral scale calculated from the autocorrelation function, decrease with latitude, ranging from ~ 100–120 km at the Equator to ~ 50 km at $55°$N (Stammer, 1997). Note, however, that some intrinsic uncertainty in the estimation of eddy length scales resides within the method chosen to define them. Over most of the subtropical oceans and along major mean fronts, seasonal variations of the eddy energy are negligible. There are, however, regions that show a pronounced annual cycle in eddy energy, notably the northern and eastern North Atlantic as well as the tropical oceans. In those locations, a strong correlation of a time varying altimetric eddy kinetic energy on annual (and longer) periods with wind stress forcing is found (Stammer and Wunsch, 1999).

3. Biogeochemical oceanic mesoscale variability: observational evidence

3.1. Measures of time/space variability

The first step towards understanding the role of mesoscale eddies on ocean biogeochemistry is to quantify the time/space variability for biogeochemical variables, based on field data, using numerical measures such as autocorrelation functions, autospectra and spatial coherence functions. Studies have estimated spatial variability, primarily of chlorophyll or its proxies, along horizontal transects using a variety of platforms from towed undulating instrumented bodies, to shipborne or moored ADCP packages, and airborne ocean color and fluorescence sensors (Yoder et al., 1993; Roe and Griffiths, 1993; Washburn et al., 1998). However, because of the strongly inhomogeneous eddy statistics in the ocean, the local results of in situ observations cannot easily be generalized while ocean colour has the potential to cover whole oceans basins with sufficient data resolution in space and time, easing examination of spectral characteristics (Fuentes et al., 2000). Near-surface chlorophyll fields for all oceans are available from satellite radiometers, based on the wavelengths and intensity of back scattered visible light from below the sea surface. Partial coverage of this field was obtained from 1978 to 1986 by the CZCS sensor and more recently, by the OCTS, POLDER and SeaWIFS sensors. Intrinsic limitations of ocean-colour data include persistence of cloudiness causing gaps in data coverage over certain regions, and inaccessibility of measuring subsurface mesoscale features. Cloudiness makes it necessary to composite many images
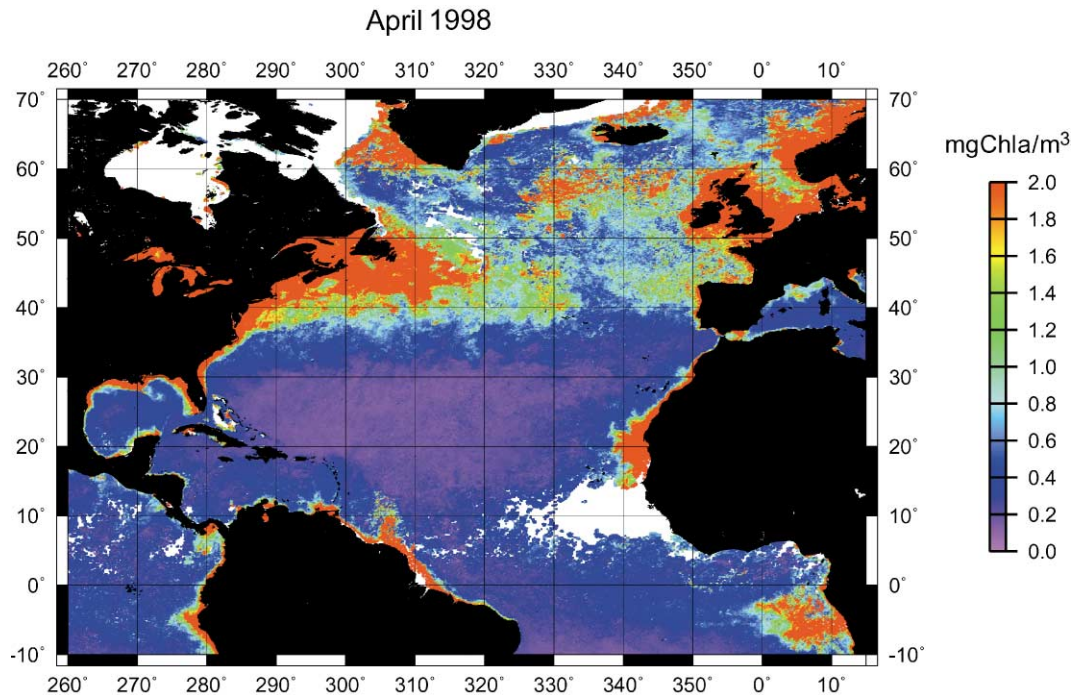

Fig. 2. Monthly composite of chlorophyll concentrations (mg/m^3) at sea surface obtained with the SeaWIFS sensor for the month of April 1998.

together. Mesoscale variability is a pervasive feature of satellite ocean-colour images and survives the 1-month compositing procedure (Fig. 2).

The impact of mesoscale features on the biology of pelagic ecosystems depends on the time-scale of the physical processes involved in comparison with that of the biogeochemical processes. Trophic levels will not respond the same way to a given physical process. Physical processes will not influence the same way a given trophic level.

Observational studies of phytoplankton have found wavenumber spectral slopes that, although varying widely, generally lie between -2 and -3 (Gower et al., 1980). Theoretical spectra also have been found to be in rough agreement with these values (Denman and Platt, 1976; Denman et al., 1977; Fasham, 1978). During NABE in April–May 1989, between $46°–51°$N and $16°–22°$W, three cyclonic eddies of different sizes (100, 200, and 270 km diameter) as observed by Geosat altimetry and hydrographic data occupied the hydrographic survey region (Robinson et al., 1993). Airborne Oceanographic Lidar (AOL) was used to estimate the chlorophyll content of the surface ocean through these eddy features (Yoder et al., 1993). Spectral analyses of the longest transects showed an average spectral slope of -2 for the laser-induced chlorophyll a fluorescence for length scales in the 1–50 km range. Recently Washburn et al. (1998) examined the spatial structure of phytoplankton and water mass properties distributions in the subpolar waters of the North Atlantic ($59°$N, $20°$W). They found autospectra of chlorophyll fluorescence varying approximately as k^{-2} (k^{-3}) for an horizontal wavenumber $k < k_t$ $(k \geqslant k_t)$, k_t being a transition wavenumber (0.145 cycles km^{-1} or 7 km, Fig. 3a) between two distinct regimes. They suggested that spatial coherence for chlorophyll fluorescence and salinity at $k < k_t$ is consistent with a regime of physical control of phytoplankton distribution at these scales where biological distributions mimic conservative tracers. At $k \geqslant k_t$, spatial coherence is lost and phytoplankton patches are controlled by the non-conservative biological sources and sinks (Fig. 3b; Washburn et al., 1998). These results are in contradiction with the spectral model of Denman and Platt (1976), which predicted a reverse picture, a transition from biological to physical control above a critical wavenumber.

As already pointed out by Fasham (1978), different processes may give rise to the same spectra, thus a note of caution is necessary here about the interpretation of spectral slopes. Indeed, the latter depend on the involved source of variance, they also can be time-dependent, and prone to sampling errors. Non-linear interactions alter spectra between different trophic levels, and usually a predator (zooplankton) has a whiter spectrum than a prey (phytoplankton), indicating that for zooplankton distributions more variance tends to exist at the smaller spatial scales (Mackas et al., 1985). In addition, Armi and Flament (1985) showed that the critical information is in the phase spectrum, not in the amplitude spectrum. Higher-order statistics such as the chlorophyll or zooplankton concentration structure function or probability distribution functions (PDF) and associated variance may provide more robust and useful measures of biogeochemical time/space variability. However, structure function methods typically require more data than spectral analyses.

3.2. Impact on biota, biogenic elements, and fluxes

Woods (1988) presented a dynamical theory for phytoplankton patchiness, which explains many features of the observed fine structure of chlorophyll concentration and opens the way to a statistical approach to predicting the large-scale distribution of primary production and its interannual variability. The theory extends classical one-dimensional treatment of the role of
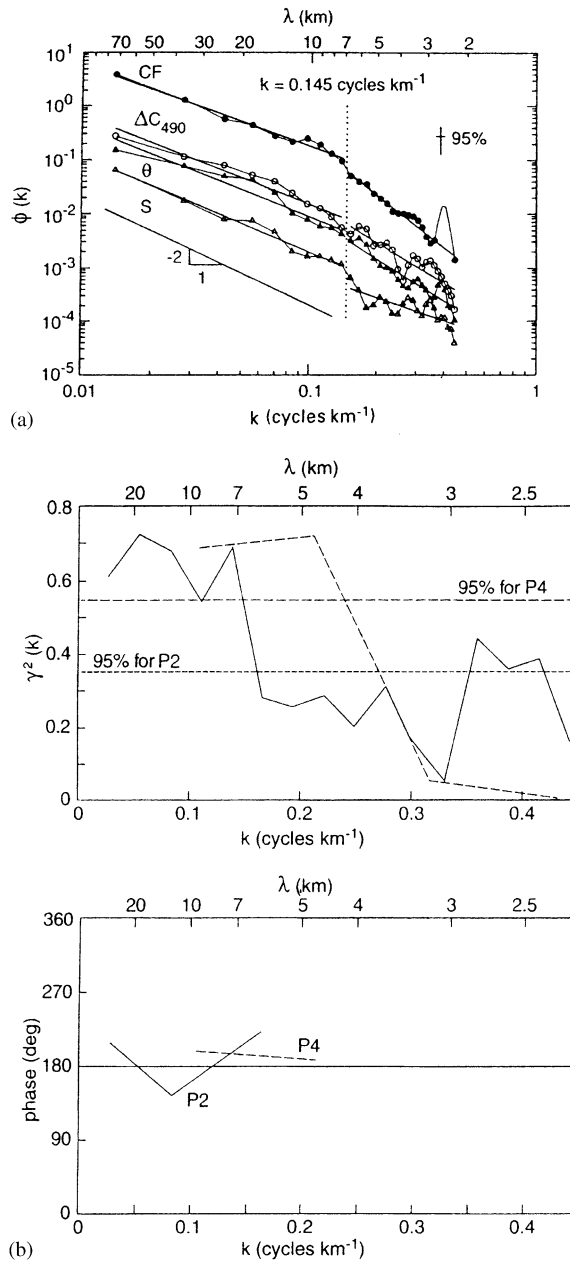
Fig. 3. (a) Autospectra ϕ for section P2 (extending from 58.5°N 19.4°W until 59.2°N 20.25°W in the Icelandic Basin) of fluorescence-derived chlorophyll [CF in (μg/l)^2 (cycles/km)$^{-1}$, filled circles], potential temperature [θ in (°C)^2 (cycles/km)$^{-1}$, filled triangles], beam attenuation coefficient anomaly at 490 nm [Δc_{490} in (m^{-1})^2 (cycles/km)$^{-1}$, open circles], and salinity [S in (cycles/km)$^{-1}$, open triangles]. Spectra are for mixed layer averages. Increases in slope occur at transition wavenumber $k \approx 0.15$ cycles/km for CF and Δc_{490} spectra. Linear fits to spectra above and below the transition wavenumber are shown with solid black lines. Points used in the fits are shown with symbols. (b) Top panel: Squared coherence γ^2 versus horizontal wavenumber k between salinity (S) and chlorophyll-derived fluorescence (CF) for sections P2 (——) and P4 (- - - - -). Section P4 extends from 59°N 21.25°W until 59.6°N 20.5°W. Bottom panel: Phase spectra for P2 and P4 between CF and S. Phase spectra are not shown where γ^2 falls below the 95% significance levels. Reproduced with Washburn et al. (1998)'s permission.

density stratification in controlling primary production to three dimensions by adopting the isopycnic gradient of potential vorticity as the dynamical variable (Woods, 1988). The evolution of the instability of a mesoscale jet is found to give rise to both the vertical transport of nutrients into the euphotic zone and subduction of biota out of the euphotic zone.

Distributions of isopycnic potential vorticity, upwelling and chlorophyll in high-resolution sections between the Azores and Greenland support the hypothesis that large-scale variation of primary production is best viewed in terms of the statistics of mesoscale events (Woods, 1988). The distribution of chlorophyll and density in the Azores front obtained by the pioneer survey of Fasham et al. (1985) can be interpreted as an isopycnic potential vorticity gradient front that passes south of the Azores and extends upstream for over 2000 km to the Gulf Stream extension. Evidence of parcels of water being subducted can be seen in sections presented by Fasham et al. (1985). Chlorophyll is observed to be transported beneath the euphotic zone and along sloping isopycnals. Similar features also are observed by Strass and Woods (1988) between the Azores and Greenland, with streamers of chlorophyll extending downwards from the top tens of metres down to 80 m. These studies all suggest substantial vertical velocities (of upwelling or downwelling) associated with mesoscale features. Vertical velocities of tens of meters per day have been confirmed at fronts by independent physical methods (Pollard and Regier, 1992). Strass (1992) reports that observed mesoscale variations of chlorophyll on the Azores-Greenland transect were associated with horizontal differences in vertical stability in spring, and horizontal gradients of isopycnal spacing and indicators of frontal upwelling in the oligotrophic summer regime, as in Woods's (1988) theory (Fig. 4).

The North Atlantic subtropical front (the subtropical convergence) southeast of the Azores supports local enhancement of chlorophyll a concentration near 34°N for latitudinal distances of the order of 1000 km (Fernandez and Pingree, 1996). High-resolution sampling of the frontal area by means of a Seasoar system showed two distinct and isolated chlorophyll patches, with values 2–3 times higher than ambient. It is explained by an increased residence time in a more favourable environment offered by the relative vertical stability due to the surface outcrop of the front and to passive biomass accumulation of motile phytoplankton cells at the front boundary. Pre-spring bloom primary production rate (March 1992) is about twice the rate for those parts of this province not influenced by frontal or mesoscale eddy processes (Fernandez and Pingree, 1996).

At 47°N 20°W, during NABE, sea-surface chlorophyll content inside the core of one of the three observed cyclonic eddies (standard eddy, diameter 200 km) was elevated by about a factor of two, which also would be consistent with increased nutrient supply in the upper ocean resulting from uplifted density surfaces in a cyclonic vortex (Robinson et al., 1993). More recently, Martin and Richards (2000) investigated vertical transport processes producing an enhanced source of surface nutrients within an anticyclonic eddy in the North East Atlantic (PRIME cruise, near 59°N 20°W). The dominant mechanism was found to be ageostrophic circulation resulting from a perturbation of the circular flow of the eddy. This can produce significant upwelling velocities (≈ 10 m/day). Other sources of nutrients were shown to be the deep winter convection thought to be responsible for its formation and wind-induced upwelling throughout the eddy.

Jenkins (1988a), and later McGillicuddy and Robinson (1997) proposed that in the oligotrophic Sargasso Sea, the time-varying eddy field might supply the required nutrients to sustain the observed primary production in the nutrient depleted gyre. McGillicuddy et al. (1998, 1999) presented high-resolution observations from moored instrumentation, and shipboard surveys,
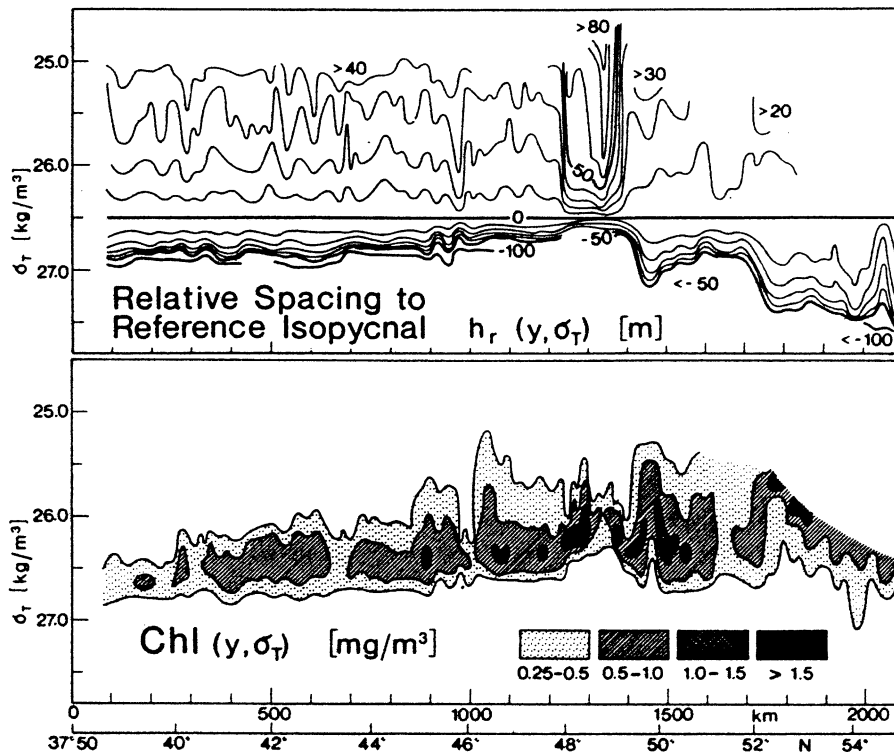
Fig. 4. Isopycnic distributions of the spacing of isopycnals relative to $\sigma = 26.5\,\mathrm{kg/m^3}$ (upper panel), and of the chlorophyll concentration (lower panel) along the section running from the Azores towards Cape Farvel, Greenland, in record B101/NOA'84, collected in late summer 1984. Data are averaged over 10 km. Reproduced with Strass (1992)'s permission.

which suggest that the vertical flux of nutrients induced by the dynamics of mesoscale eddies — the eddy upwelling mechanism (Fig. 5a) — was indeed sufficient to balance the nutrient budget in the Sargasso Sea by accounting for 40–73% of the total nitrate supply. The Bermuda Testbed Mooring, equipped with state-of-the-art new instruments, allowed the collection of a high-resolution, long-term data set sampling periodic as well as episodic processes (Dickey et al., 1998). Fig. 5b illustrates the passage of such an episodic eddy nutrient pumping event, described in detail by McNeil et al. (1999). Siegel et al. (1999) completed an analysis for the BATS station (32°N, 64°W), where they combine observed sea level anomalies (SLA) from the merged T/P-ERS missions, hydrographic estimates of dynamic height anomaly, and BATS nitrate–density relationship to remotely deduce upper ocean isopycnal displacements and the nitrate flux into the euphotic zone due to eddy pumping.

A drifter survey in the weak mesoscale hydrodynamic variability region of the North Equatorial Current at 18°N 30°W (Fig. 1) showed a hydrodynamic situation characterized by small-scale variability; the most interesting feature was the intrusion of nutrient-depleted Subtropical Salinity Maximum Water ($S_{\max}$) in the euphotic zone (Jochem and Zeitzschel, 1993). Koeve et al. (1993) reported mesoscale variability in the depth of the nitracline, where nitrate was already depleted in
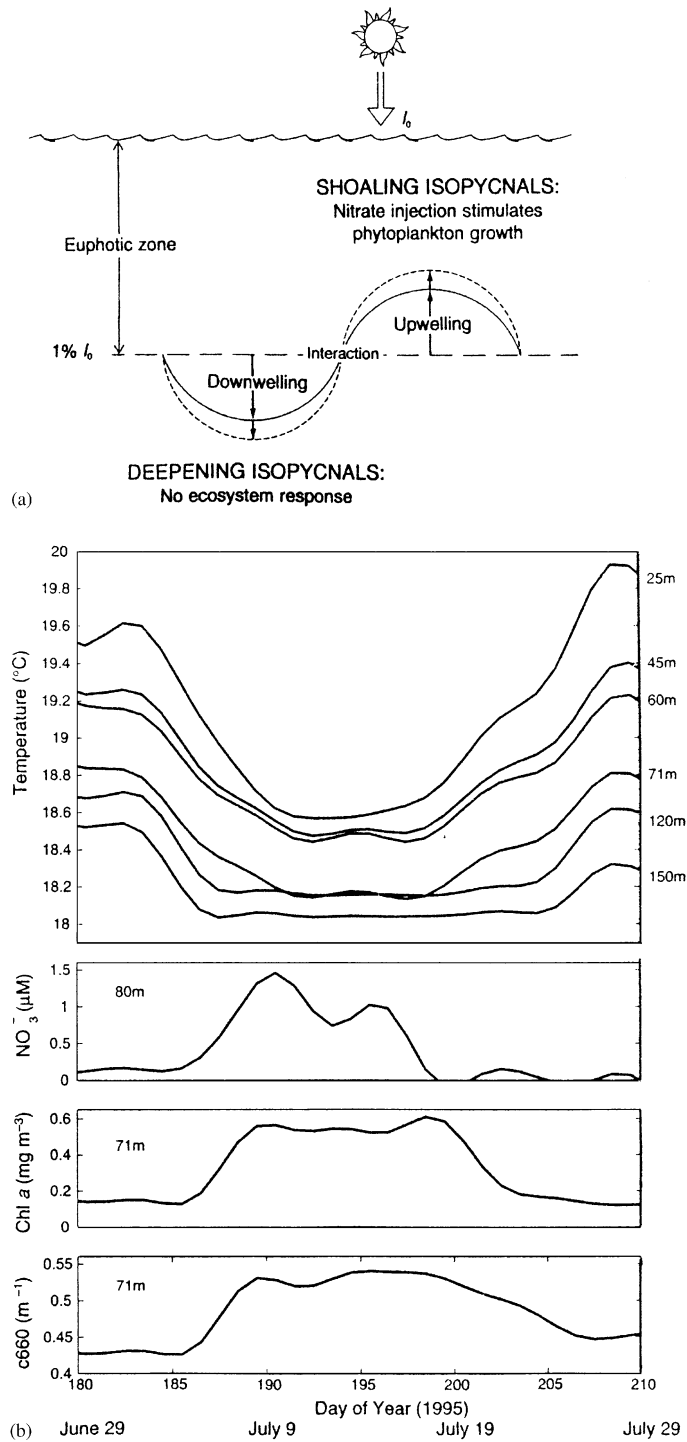
Fig. 5. (a) Schematic representation of the eddy-induced upwelling mechanism. I_0 represents incident solar radiation, and 1% I_0 the base of the euphotic zone. (b) Results from the Bermuda Testbed Mooring 3rd Deployment during the summer of 1995. All signals have been filtered via a 6-day moving average. Reprinted by permission from Nature (McGillicuddy et al., 1998) copyright 1998 Macmillan Magazines Ltd (www.nature.com).

the surface layer. This depth was indeed dependent on the occurrence/non-occurrence of the subsurface subtropical salinity maximum. Frequent occurrence of this S_{max} suggests higher variability of new production and *f*-ratio than usually expected for oligotrophic regions.

Particle fluxes to a sediment trap at depth are observed as a function of time at a fixed point in space. Such a trap can be considered to collect particles from a certain seawater volume, which is a function of vertical and horizontal transport vectors. A Lagrangian analysis of particles settling through a random mesoscale eddy field indicates that the potential sea-surface source area of a trap sample is a function of the mean vertical settling rate of the particles and the mesoscale eddy field above the trap (Siegel et al., 1990; Siegel and Deuser, 1997). Newton et al. (1994) showed that the timing and magnitude of the 1989 NABE spring bloom settlement was indistinguishable in two sediment trap sites (trap depths of 3100 and 3700 m), located 100 km apart, near 48°N 20°W, indicating no spatial variability in flux between these sites. In contrast, the 1989 autumn flux event was barely recorded at one of the sites. Given the biogeochemical importance of this latter event to deep waters, most notable in terms of its contribution to POC flux, this observation of deep-water mesoscale flux variability indicates that the signature of surface mesoscale biological–physical coupling propagates all the way to the bottom, affecting the time and space scales of ocean biogeochemistry throughout the water column (Newton et al., 1994). Waniek et al. (2000) determined characteristics of the statistical funnel and catchment areas above moored deep-ocean sediment traps deployed at the Biotrans site (47°N, 20°W). They showed that, at a given mooring site, assemblages of sinking particles sampled at different depth horizons over the same time interval may originate from independent epipelagic systems having experienced distinct bloom phases. A careful interpretation of particle flux data would require a good knowledge of the rates of sinking and remineralization as well as of the three-dimensional physical environment in the mooring site region.

Measurements of individual pigment levels in the water column, in sedimenting material and in faecal material, help to elucidate the pathways of pigment degradation and hence carbon utilization and export flux into the ocean. During the 1990 spring bloom at 37°N 20°W, drifting sediment traps appeared to be in a jet moving southwesterly along a water mass front between eastern basin water (to the north) and North Atlantic Central Water (to the south) and which seemed to be drawing in water from both of these water masses (Head and Horne, 1993). Measurements of pigments indicated that areas of downwelling, thought to be associated with these convergent currents, may have accelerated the drawing down of the least motile and/or least healthy phytoplankton cells, leading to flocculation and consequently enhanced sedimentation rates.

3.3. Community structure

The effect that mesoscale features have on a resident plankton community will clearly depend on the gradients in nutrients and phytoplankton initially present and on the intrinsic biological reaction rates. Phytoplankton with a rapid growth rate will benefit from arriving within a patch of nutrient-rich water, possibly at the cost of a previously dominant species that thrived on an ability to do better with low nutrient levels in the long term and which lacks the opportunistic edge. In addition to the complex effect on planktonic distribution and productivity, the effect on the community structure may be significant.

A first report of horizontal and vertical distribution of nutrients, phytoplankton, and bacterio-plankton in a cold-core eddy in the Northeast Atlantic was given by Lochte and Pfannkuche (1987) at 48°N 22°W. The cold core was different from ambient northeast Atlantic waters in terms of nutrient chemistry, phytoplankton species, distribution and abundance, bacterial numbers and cell size, and in processes determining the phyto- and bacterioplankton abundance. Highest concentrations of chlorophyll *a*, total phytoplankton biomass, dinoflagellates and bacteria were observed in the surface water of the eddy center. Karrasch et al. (1996), during NABE, observed that simultaneously and side by side, an autotrophic and a heterotrophic-dominated system could be supported by prevailing hydrographic conditions. At 47°N 20°W, two different mesoscale structures were sampled, dividing the drift experiment into a cyclonic and anticyclonic phases. Indeed, the combined bacterial biomass dominated within the mixed layer during the anticyclonic phase, while the cyclonic phase was dominated by eucaryotic phytoplankton. A shift of biology toward the microbial food web was indicated by a strong increase of bacteria during the anticyclonic phase. Apparently, the spring bloom in the North Atlantic does not follow precisely the ideal picture of a northward moving bloom, but rather forms a patchwork representing different bloom stages within mesoscale features (Karrasch et al., 1996). The observation of co-occurrence of autotrophic and heterotrophic systems may produce an export of C and N by sedimentation from the productive zone to depth, which may be variable in space and time (Newton et al., 1994). In the subtropical front-Azores Current (AC) system, a high-resolution survey across this front showed chlorophyll *a* fluorescence associated with the southern frontal boundary consisting of chain forming diatoms and flagellates, and the fluorescence associated with the AC, made up of cells in the less than 2 μm size-class, respectively (Fernandez and Pingree, 1996). There was also evidence that the phytoplankton species composition within this frontal region has affinities with the Sargasso sea, as befits the Azores Current, which has its root in the Gulf Stream.

The intensive field observational phase of JGOFS in the North Atlantic ocean together with the advent of remotely sensed data and new emerging in situ observational technologies have served to highlight the importance of oceanic mesoscale variability on biogeochemical cycles and on the strength of the ocean biological pump. The most significant effects are on spatio-temporal distributions of phytoplankton, zooplankton and associated nutrients, and also on biological production and export to the deep ocean. Several issues deserve special attention: synopticity in mesoscale oceanographic surveys, "capturing" the observed ecological response (species distributions, trophic structure, food web dynamics) resulting from the presence of mesoscale features, and quantifying more robust measures of the ecosystem/physical system beyond bulk measures on appropriate time and space scales (e.g. plankton physiological state, vertical velocities, species distributions).

4. Biogeochemical oceanic mesoscale variability: modelling studies

According to Charney's (1971) theory for geostrophic turbulence, enstrophy (variance of vorticity) cascades from the source scale of the main energy and enstrophy input through the mesoscale inertial range towards smaller scales. The main energy and enstrophy input results from baroclinic instability of gyre scale fronts. This cascade implies sharpening of gradients and intensification of fronts. The flow pattern associated with frontogenesis is explained by the conservation law of

potential (relative and planetary) vorticity. Prerequisite of frontogenesis inducing jet acceleration and vertical circulation is the existence of gradients of dynamically active variables (active tracers).

Since Denman and Gargett's review (1995) on biological and physical interactions in the upper ocean, recent research has been devoted to study the effect of hydrodynamical mesoscale processes on planktonic ecosystems in either process models, regional or basin-scale models of the North Atlantic ocean (McGillicuddy et al., 1995; Smith et al., 1996; Dadou et al., 1996; McGillicuddy and Robinson, 1997; Spall, 1997; Oschlies and Garçon, 1998, 1999; Spall and Richards, 2000a; Martin et al., 2000; Mahadevan and Archer, 2000).

4.1. Process models

Spall (1997) and Spall and Richards (2000a) examined the effect of a developing instability of an open-ocean mesoscale jet on local ecosystems at the contrasting sites of BATS and NABE (47°N 20°W) with a primitive equation physical model coupled with a slightly modified Fasham et al. (1990) ecosystem model. The summer months were selected for simulations since they constitute the period when any vertical fluxes of nutrients are capable of stimulating increased production because phytoplankton growth is nutrient limited. An equally important criterion was that the ecosystem would be near steady state during this period, easing the diagnosis of the influence of physical processes. At both sites, the action of upwelling and subduction introduces spatial heterogeneity in the plankton biomass and primary production at a variety of length scales (Fig. 6). Length scales are of the order of a few km for filamentary structures, up to 50 km for coherent eddy and subducted features. The action of the instability of the frontal jet is to advect water parcels along strongly sloping isopycnals, giving large vertical transports. When the vertical transports act to bring nitrate into the euphotic zone, features with the signature of high new production are formed. These features take the form of thin filaments drawn from the meanders, and coherent eddy features with strong vertical transports associated with their formation. When vertical transports are in the opposite sense, advecting biota down sloping isopycnals, remnant populations of plankton are transported beneath the euphotic zone. This plankton is destined for depletion by mortality and grazing losses, but the appearance of the plankton signal will be dependent on the physical time-scale of the subduction in comparison with the time-scale of these losses. At both sites, the increase in primary production can be locally of the order of 100%, and of the order of 10% when averaged over the frontal region with the majority a result of increase in new production.

The ecosystem response is shown to be sensitive to the frontal set-up (Spall and Richards, 2000a). One set-up, referred to as the strong front, was based on the hydrographic data from the FASINEX cruise in the Sargasso Sea (Pollard and Regier, 1992), showing strong isopycnal thickness gradients. Cross-frontal transport occurs forming coherent features. In a second frontal set-up, referred to as the weak front, with moderate gradients in isopycnal thickness, fitted with hydrographic data from the Azores region (Fasham et al., 1985), there was a barrier to mixing across the jet axis. Cross-frontal mixing is fundamental if large reactions of the ecosystem to the frontal dynamics are to be expected.

Spall and Richards (2000a) used particle tracking in the flow field to trace the trajectory of water parcels and their associated biological evolution. Figs. 7 and 8 clearly show that the vertical movement of nitrate occurs only during the formation of the eddy (around day 33 right
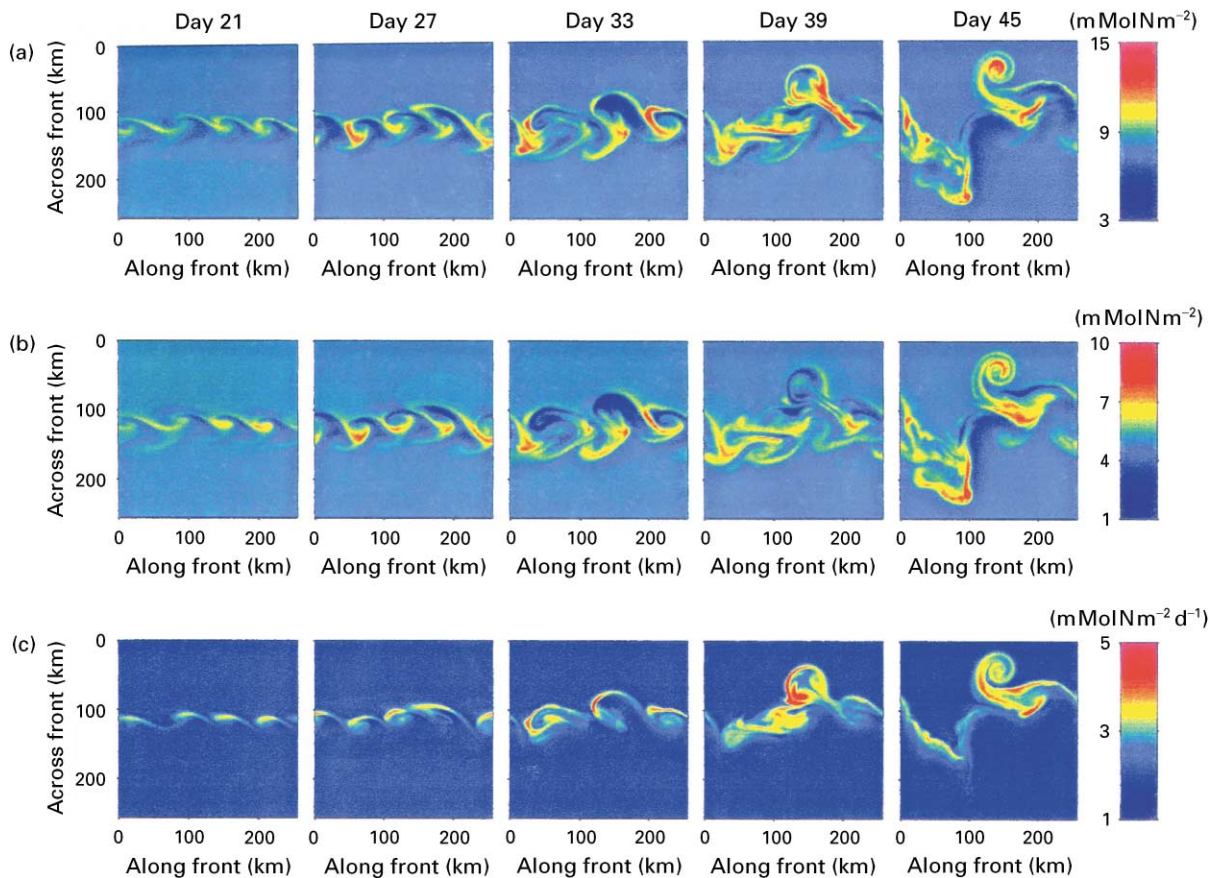
Fig. 6. Time-series of model depth integrated fields (mmol N/m^2) for BATS in the strong front configuration (see text for explanation). (a) Phytoplankton, (b) Zooplankton and (c) Primary production. Reproduced with Spall and Richards (2000a)'s permission.

at the front). After the eddy detaches and moves into the oligotrophic region, no new vertical motion inside the eddy is simulated and no new nitrate is pumped in, although the eddy moves by about one diameter distance between days 39 and 45. This would suggest that horizontal movement of nitrate by eddies may be an important process to transport nitrate into oligotrophic waters.

Following up Spall and Richards (2000a), Martin et al. (2000) recently investigated the community structure of a two-size class planktonic ecosystem in an unstable frontal region typical of the Sargasso Sea. Confirming previous work, they show that an unstable front boosts primary production locally by in excess of 10%, and that this percentage may be much higher depending on the background nutrient profile. Differences between the phytoplankton in parameters governing nutrient uptake and mortality lead to striking shifts in community structure when coupled to vertical transport resulting from the frontal dynamics. These shifts in community structure did not result in a change in total primary production. Competition was found to partition production not to alter its total value. The nature of these shifts is also sensitive to the background nutrient profile.
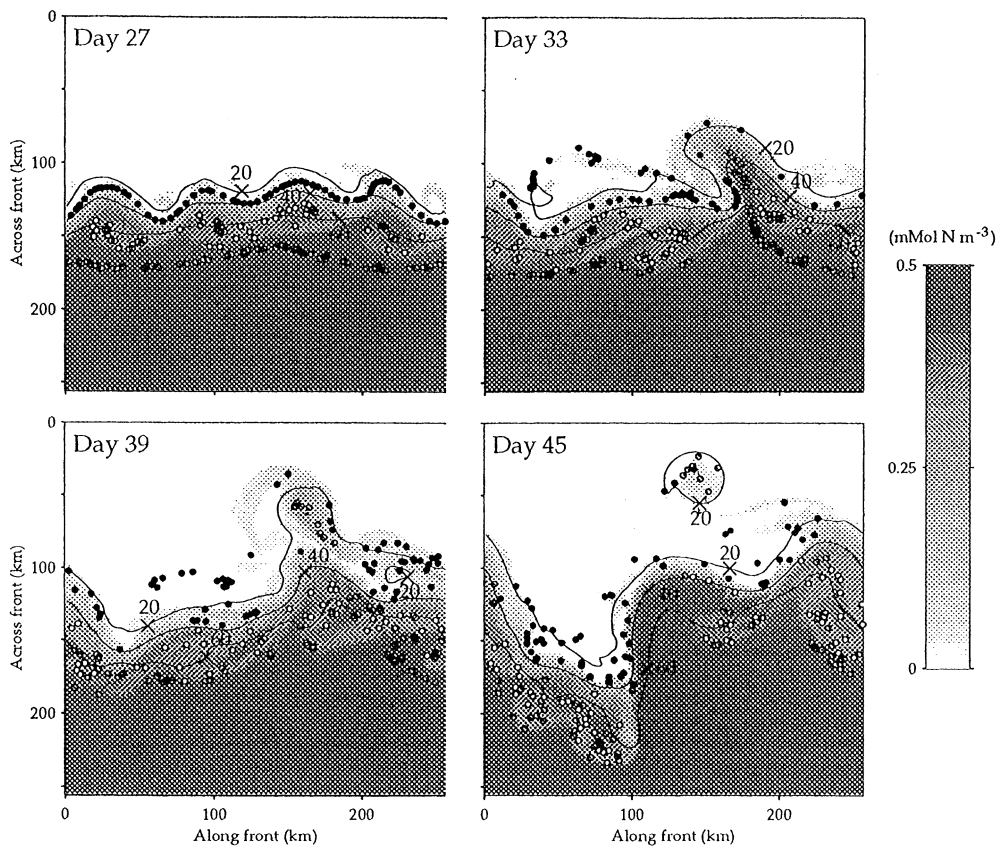
Fig. 7. A time-series of nitrate concentration in the $\sigma = 25.10\,\text{kg/m}^3$ isopycnal for the strong front, with the positions of seeded particles. Contours are the depth of the isopycnic layer with a contour interval of 20 m. Reproduced with Spall and Richards (2000a)'s permission.

A model of the meandering of the North Equatorial Current (Dadou et al., 1996) finds that, when eddies are resolved in an idealized domain, the mean values of primary and export productions in the North Equatorial Current jet zone are doubled. Upwelling located at the edge of eddies can increase phytoplankton biomass by up to 33%. This is consistent with other modelling studies of eddy–eddy interactions (Yoshimori and Kishi, 1994; McGillicuddy et al., 1995). Such eddy interactions produce convergent flow and can generate a frontal jet between eddies. The associated vertical velocities are responsible for an increased flux of nutrients into the euphotic zone and an associated increase in phytoplankton biomass. It is highlighted by Yoshimori and Kishi (1994) that it is the time evolution rather than the magnitude of the vertical velocities that is most important for biomass accumulation.

Smith et al. (1996) investigated another potential source of chlorophyll patchiness, the mixed-layer variability using a quasi-geostrophic mixed-layer model coupled with Fasham et al.'s (1990) ecosystem model in an open-ocean typical of the North Atlantic drift at 50°N. They examined how spatial variations in the depth of the mixed layer (ML) caused by the eddying motions can affect the amount of photosynthetically active radiation on a cell, thereby affecting production rates.
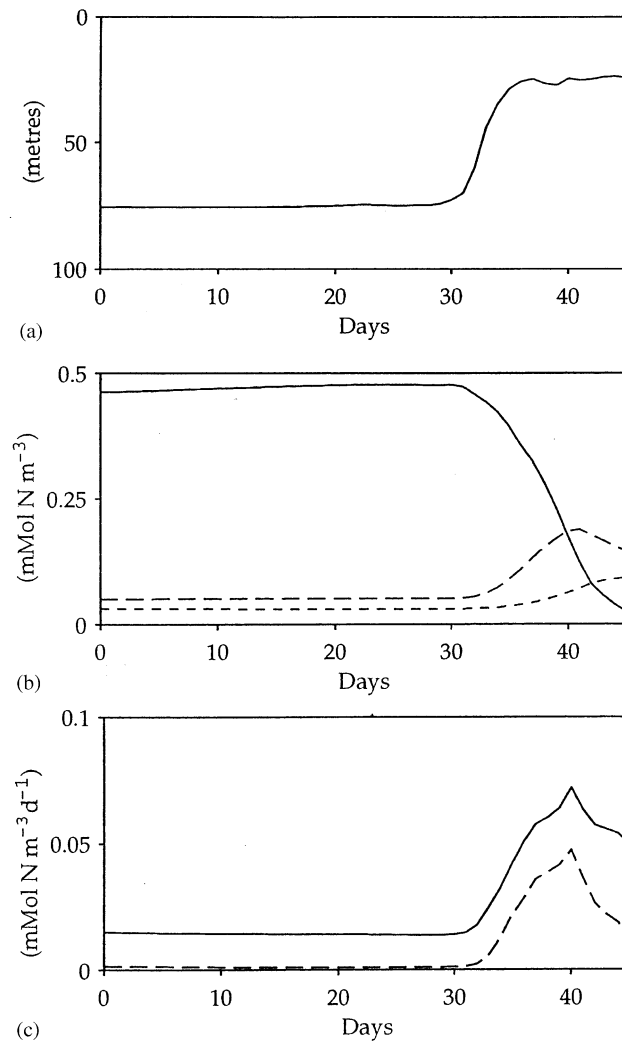
Fig. 8. Ensemble mean fields following particles that are observed in the eddy feature on day 45 (a) Depth (b) Phytoplankton concentration (long dashed line), nitrate concentration (solid line) and zooplankton concentration (short dotted line) (c) Total primary production (solid line) and new production (dashed line). Reproduced with Spall and Richards (2000a)'s permission.

Somewhat surprisingly, the net effect of eddies on overall rates of annual regional primary production was found to be small between simulation with and without eddy variability ($\approx 2\%$). They caution, however, that they applied relatively modest perturbations to the dynamics of the ML depth, and conclude that studies with greater distortion should be performed.

4.2. Regional models

McGillicuddy and Robinson (1997), using a simplified biological model embedded in a regional eddy-resolving model, constructed long-term aseasonal simulations characteristic of the mesoscale

environment in the Sargasso Sea to study mechanisms by which eddy processes can transport nutrients into the euphotic zone. They identified a particular mechanism that appears to account for the bulk of the nutrient supply necessary to sustain levels of new production inferred from tracer observations in the Sargasso Sea (Jenkins, 1988a; Jenkins, 1998). Density surfaces are perturbed vertically by the formation, evolution and destruction of mesoscale features. Shoaling density surfaces lift nutrients into the euphotic zone, which are rapidly utilized by the biota. Deepening density surfaces serve to push nutrient-depleted water out of the well-illuminated surface layers. The asymmetric light field thus rectifies vertical displacements of both directions into a net upward transport of nutrients, which are fixed into organic material. This upward flux must be balanced by a commensurate export of that material or its derivative products. McGillicuddy et al. (1998) confirmed their previous findings by combining use of in situ biogeochemical and physical data and a satellite-based statistical model.

The magnitude of the nutrient flux induced by this eddy upwelling mechanism depends critically on the amplitude of the vertical displacements of fluid at the base of the euphotic zone. Realistic simulation of this process requires explicit resolution of the baroclinic structure of the upper ocean. This is particularly crucial in areas such as the Sargasso Sea, where the mean current profile causes eddies to be surface intensified (McWilliams, 1974). Although the depth-integrated eddy kinetic energy is not sensitive to the details of the near-surface expressions of the eddies, the biogeochemical ramifications depend critically on this aspect. Achieving the simulation of a proper vertical distribution of that energy is thus a necessity.

The effectiveness of the eddy-induced upwelling mechanism also firmly depends on the remineralization depth and time-scale of the organic matter versus the occurrence time-scale of the eddy features. Let us imagine a Lagrangian one-dimensional water column. If isopycnals from below the euphotic zone are moved up into the light, phytoplankton can utilize new nutrients for photosynthesis. These nutrients will be converted into organic matter and part of it will sink out of the euphotic zone. Thereby organic matter will be removed from the isopycnal and be remineralized further down in the water column. The critical point is now how nutrient concentrations on the isopycnal can recover before a second eddy will move it up into the euphotic zone again. If water columns were circulating in a vertically coherent manner through the ocean, then the eddy-pumping mechanism would essentially only work once. Its effect in the subtropical ocean would be to deepen the zone of nutrient depletion to the deepest isopycnal that during eddy events reaches the euphotic zone. The bottleneck for nitrate supply would simply be moved to a greater depth at which eddies can not provide sufficient doming. McGillicuddy and Robinson (1997) pointed out that organic matter remineralization in the subtropical gyre may be faster (of the order of 3 months for the nitrate restoring time-scale below the euphotic zone) than an eddy lifetime (of the order of half a year). However, Siegel et al. (1999) identified in altimetric sea-level anomalies time series over 3 years at BATS 18 individual upwelling events, each with a mean duration of 23 days and a mean time between events of 31 days. This yields a required remineralization time-scale within the aphotic zone very close to the uplifting events time-scale.

Recently, Mahadevan and Archer (2000) used a simplified biological model embedded in a regional-eddy-resolving model of the BATS area. Using three resolutions (0.4°, 0.2°, and 0.1°), they showed that only when they started to resolve features at the Rossby scale and smaller did the production start to increase.

4.3. Basin-scale models

Oschlies and Garçon (1998) extended these regional environments modelling studies to a basin-scale environment, the North Atlantic basin, thereby spanning distinct regimes of primary production and eddy variability. The model covers the equatorial and North Atlantic ocean between 15°S and 65°N, with a grid spacing of $\frac{1}{3}°$ in meridional and $\frac{2}{5}°$ in zonal directions, and has 37 levels in the vertical of which 11 are situated in the upper 150 m. The pelagic ecosystem model is a simple four-component (nitrate, phytoplankton, zooplankton, detritus) nitrogen-based model (Oschlies and Garçon, 1999). Although the grid resolution is not yet fine enough to correctly reproduce eddy scales north of about 30°N (Stammer and Boning, 1996), the model is a useful tool to study the impact of mesoscale variability in the subtropical gyre.

Three numerical experiments have been carried out with differing levels of eddy activity (see Oschlies and Garçon, 1998): a viscous experiment with high horizontal viscosity that effectively damped out mesoscale activity, an eddy-permitting control experiment in the standard configuration with biharmonic horizontal friction, and an assimilation experiment that used mapped sea-surface height observations taken at 5-day intervals from the combined TOPEX/POSEIDON and ERS-1 altimetric missions to closely reproduce observed eddy activity in the model (Oschlies and Willebrand, 1996). The comparison of these three numerical experiments showed that, in response to an increase in eddy activity, the region of low new and primary production in the subtropical gyre was reduced. For example, the simulated annual primary production is displayed in Fig. 9 for the viscous, control, and assimilation experiments. A pronounced feature of all simulations is the region of much too low primary production (< 1 g C/m^2/year). While similarly low values also were simulated by the coarse-resolution model of Sarmiento et al. (1993), it was originally hoped that an increase in resolution and hence in eddy activity would significantly improve the model results. Fig. 9, as well as the results of Oschlies and Garçon (1998), clearly show that the increase in eddy activity represented in this model alone cannot bring simulated production rates in the oligotrophic subtropical gyre close to observed levels.

While eddy-induced nutrient supply by simple vertical displacement of isopycnals might play a role, other mechanisms of eddy-induced transport have to be considered as well. An alternative possible contribution of eddies might arise from their ability to transfer properties horizontally across stream lines of the mean flow. This may be of particular importance for the subtropical gyre where mean currents tend to circulate around the oligotrophic gyre's interior. In analogy to the Ekman-transport mechanism investigated by Williams and Follows (1998), eddies could bring nutrients horizontally across the mean geostrophic flow into the subtropical gyre.

While at least in the centre of the oligotrophic subtropical gyre eddies do not have much impact in the numerical model, largest changes in new and primary production occur at the periphery of the oligotrophic region (Oschlies and Garçon, 1998). The narrowing of the low (< 1 g C/m^2/year) primary-production region with increasing eddy activity (Fig. 9) in principle can be caused by both vertical and horizontal input of nitrate into the euphotic zone. The individual supply routes of nitrate into the upper 126 m, which in the z-level model is taken as proxy for the euphotic zone, are shown in Fig. 10 for the region 12°–30°N and 70°–22°W and for the three experiments differing only in the level of eddy activity. Obviously there is a steady increase in nitrate supply by vertical turbulent mixing from the viscous experiment to the control and assimilation experiments. This is accompanied by a simultaneous increase in horizontal transport. The nitrate flux by vertical
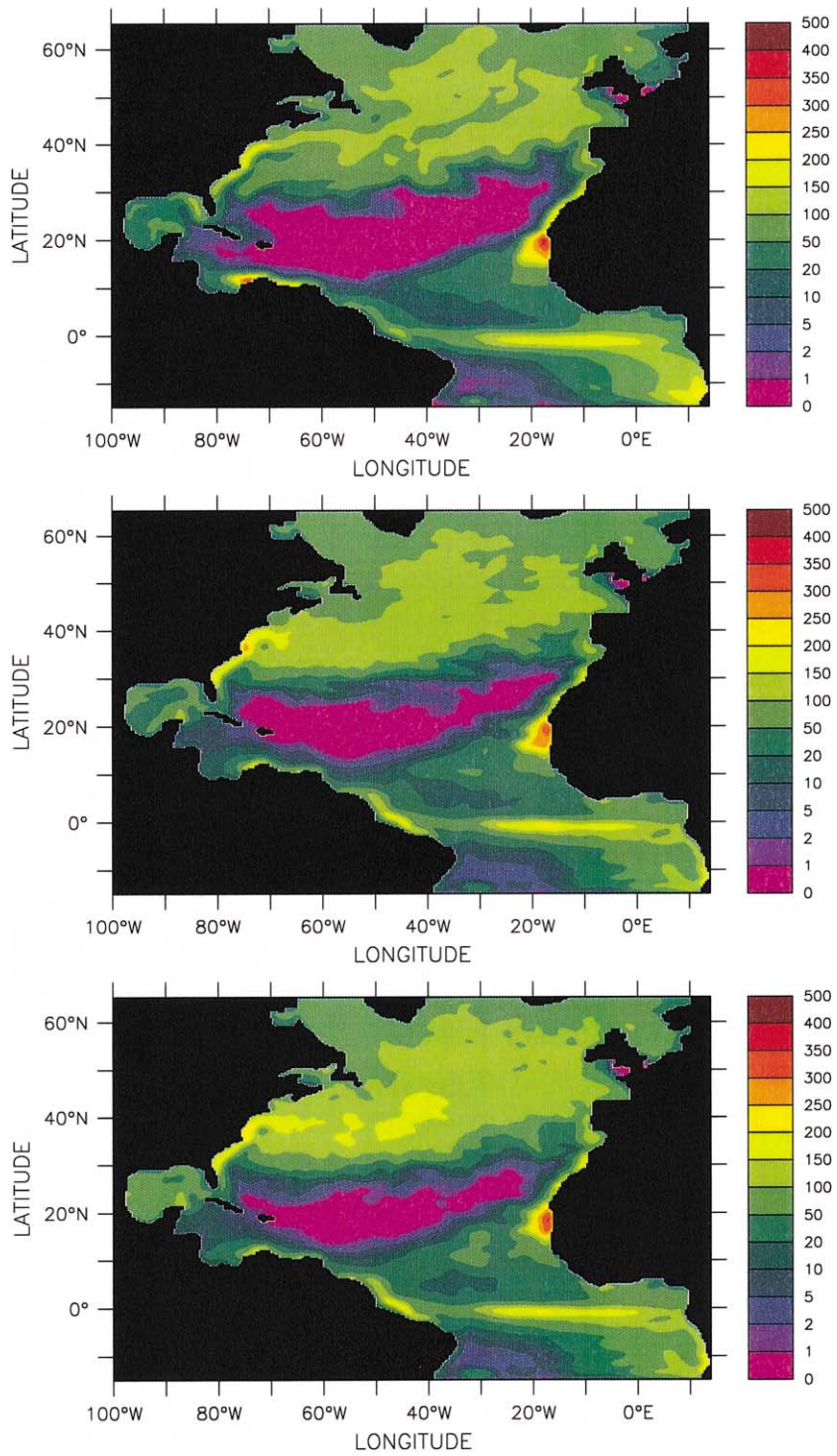
Fig. 9. Primary production in the viscous (upper panel), control (middle panel), and assimilation (bottom panel) simulation experiments (g C/m²/year).
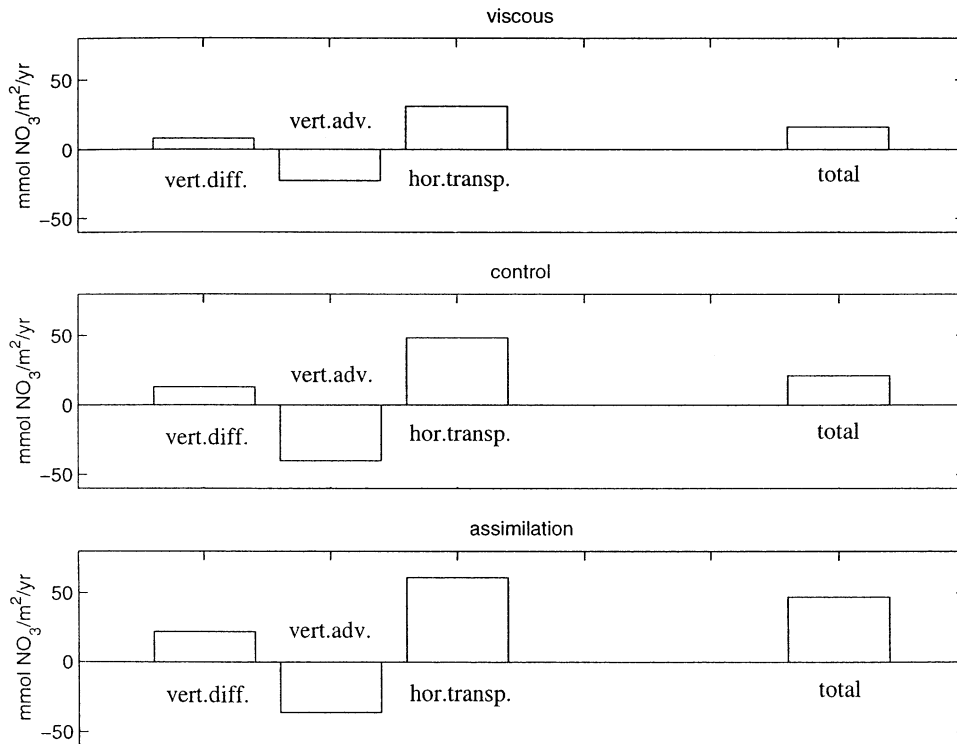
Fig. 10. Supply routes of NO_3 in the upper 126 m for the region 12°–30°N and 70°–22°W in the viscous, control and assimilation experiments.

advection is negative in all experiments, indicating the dominance of Ekman pumping and associated downwelling of nutrients in the subtropical gyre. Surprisingly, the vertical advective loss is smallest in the run with lowest eddy activity. Increasing the level of mesoscale variability tends also to enhance the vertical export of nutrients. At least in the subtropical gyre regional average, the model results seem to indicate that the eddy-induced horizontal transport of nitrate predominates over the eddy-induced upwelling mechanism, being consistent with Spall and Richards (2000a) process model results. The traditional picture in biogeochemical cycling is the vertical balance, but transfer of biogeochemical tracers across gyres boundaries does play a role through geostrophic eddies and horizontal Ekman flow. While eddies act to diffuse nitrate down the gradient in oligotrophic regions, the transport distance might be limited by the planktonic nitrate consumption time. However, if one considers advection of particulate and dissolved organic nitrogen, eddy-induced nitrogen fluxes are not necessarily restricted to nitrate, and hence could act over much longer distances as one would assume from a nitrate-consumption time-scale only. Indeed, Bauer and Druffel (1998) showed that dissolved organic carbon and suspended particulate organic carbon inputs from ocean margins to the open-ocean interior may be more than an order of magnitude greater than inputs of recently produced organic carbon derived from the surface ocean.

The mechanisms for eddy-induced transport subdivide by the main orientation of the fluxes, either vertical (submesoscale upwelling along fronts, eddy formation/interactions, and interactions

Table 1
Annual nitrate input (in mmol NO_3/m^2/year in the upper 126 m) per region and transport route in the viscous (V), control (C), and assimilation (A) experiments. (Numbers from Oschlies and Garçon (1998) modelling study)

Region	Experiment	Vertical diffusion	Vertical advection	Horizontal transport	Total
North Atlantic 8°–65° N	V	212	37	10	259
	C	195	76	17	288
	A	245	76	19	340
Subpolar North Atlantic 50°–65°N	V	434	11	− 65	380
	C	296	98	− 4	390
	A	307	99	9	415
Mid-latitudes North Atlantic 30°–50°N	V	388	− 28	40	400
	C	402	27	53	482
	A	533	10	41	584
Subtropical gyre 12°–30°N, 70°–22°W	V	8	− 23	31	16
	C	13	− 40	48	21
	A	22	− 36	61	47
Canary Basin 8°–30°N, 22°W-coast	V	9	330	129	468
	C	12	214	204	430
	A	20	236	170	426
Gulf of Mexico 18°–32°N, 100°–82°W	V	49	206	− 31	224
	C	56	414	− 204	266
	A	107	492	− 226	373
Equatorial Atlantic 8°S–8°N	V	31	462	− 91	402
	C	56	457	− 149	364
	A	56	474	− 156	374

of wind-driven currents with the mesoscale field) or horizontal (eddy fluxes from periphery of oligotrophic gyres). Modelling is the only tool to provide an assessment of the regional balances between horizontal and vertical eddy-induced nutrient supplies. Table 1 shows, for one peculiar modelling study, that in other biogeographic provinces than the subtropical gyre in the North Atlantic, the modelled vertical route for supplying nitrate in the euphotic zone seems to dominate the horizontal transport.

The influence of mesoscale dynamics on biological production (new, regenerated, total) and export to the deep ocean as predicted by the above-mentioned modelling studies can be summarized in Table 2. Obviously, Table 2 cannot provide a basis for a quantitative intercomparison between the tabulated model simulations due to their distinct nature. Rather it gives the relative contribution of eddies to key biogeochemical properties. Despite the conflicting numbers, which indicate the diversity of studies and present uncertainty, the presence of eddies generally contributes to enhance the biological productivity. Few estimates of the effect of export production are available, but they emphasize the crucial need for further quantification of the influence on biogeochemical fluxes. A number of key questions remain to be addressed in the future: Are the scales required for modelling physics sufficient for the biology? Can we reach resolution "closure" with respect to biological/physical interactions? How does remineralization in the shallow aphotic

Table 2
Summary of the net impact of modelled eddies on estimates of new, regenerated, total primary and export production (as POC export). The positive sign means an increase, a negative one a decrease in the quantity. To know the nature of the base case for each study, please see text

Region	New production (%)	Regenerated production (%)	Total primary production (%)	POC export (%)	References
North Atlantic 8°–65° N	+ 31		+ 25	+ 24	Oschlies and Garçon (1998)[a]
Subpolar North Atlantic 50°–65°N	+ 8		+ 7	+ 6	Oschlies and Garçon (1998)[a]
Mid-latitudes North Atlantic 30°–50°N	+ 45		+ 40	+ 36	Oschlies and Garçon (1998)[a]
North Atlantic drift province 50°N	+ 1	− 6	− 2		Smith et al. (1996)
NABE area 47°N 20°W			+ 6		Spall (1997)
NABE area 47°N 20°W	+ 50		+ 25		Martin et al. (2000)
Subtropical gyre 12°–30°N 70°–22°W	+ 200		+ 140	+ 200	Oschlies and Garçon (1998)[a]
BATS area 32°N 64°W	+ 100				McGillicuddy and Robinson (1997)
BATS area 32°N 64°W	+ 65				McGillicuddy et al. (1998)
BATS area 32°N 64°W	+ 43				Oschlies and Garçon (1998)[a]
BATS area 32°N 64°W	+ 137	− 2	+ 9		Spall and Richards (2000a); Spall, pers. com.
BATS area 32°N 64°W	∼ 50		+ 10		Martin et al. (2000)
Canary Basin 8°–30°N 22°W-coast	− 8		− 3	No effect	Oschlies and Garçon (1998)[a]
EUMELI oligotrophic site 21°N 31°W			+ 100	+ 100	Dadou et al. (1996)

[a]Oschlies and Garçon (1998) numbers refer to the viscous and assimilation experiments (see text).

zone vary on the mesoscale, and does subsurface resupply of nutrients limit the effectiveness of eddy transport in the vertical?

5. How to quantify the role of mesoscale variability on plankton dynamics?

During the JGOFS synthesis phase, modelling has become a key tool for interpretation (testing scenarios), extrapolation and prediction, and is playing an essential role for achieving this synthesis. Satellite remote sensing is the other method potentially capable of delivering synoptic descriptions of the ocean's state on a basin or global scale. Simultaneity of the POLDER, OCTS, SeaWIFS ocean color sensors and the TOPEX/POSEIDON (T/P) and ERS-2 altimeters provides the very first opportunity to analyse the large-scale distribution of phytoplankton biomass in relation to the forcing caused by the physical environment. To quantify the role of mesoscale

variability on plankton dynamics means to understand what is observed, and to be able to model the underlying processes creating those biogeochemical mesoscale features in order to determine the relative role of each process involved. The combination of complementary remotely sensed and in situ data with numerical coupled physical–biogeochemical models through assimilation can offer the context in which the issue of the quantitative effect of intermittent mesoscale features on biological production and export to the deep ocean can be addressed. Although intermittent, these filamentary and/or coherent physical features may indeed make a significant contribution to the strength of the biological pump.

Assimilation of high-resolution data sets like those obtained by altimeter and ocean-color missions into eddy-resolving basin-scale-coupled biological and physical models will produce an enhanced understanding of mesoscale processes and their role in biogeochemical water property transport. Present efforts to combine altimeter and ocean-color data with primitive equation models concentrate on the development of practical methods to deal with the problems of constraining the deep ocean by surface observations in a dynamically and consistent way, and the technical difficulties posed by the huge dimension of the ocean state and its error covariance. Data assimilation, still in an early developmental stage in coupled marine biogeochemistry modelling, has made significant progress with a preferential use of inverse methods. These have been used mainly to estimate poorly known biological parameters (Evans and Fasham, 1995; Matear, 1995; Lawson et al., 1996; Hurtt and Armstrong, 1996,1999; Spitz et al., 1998; Evans, 1999; Gunson et al., 1999; Schartau et al., 2000). Estimation of biological parameters, and hopefully of parameterizations, consistent with in situ biogeochemical data and/or ocean-color data will increase our confidence in the performance of the ecosystem models.

Any attempt to quantify the effect of mesoscale features should follow a different strategy depending on which spatio-temporal scale one wishes to quantify. At the local or regional scales, one can use fully eddy-resolving coupled biological physical models, implying a resolution down to a few kilometers (5–10 km). At the basin scale, $\frac{1}{10}^{\circ}$ resolution circulation models of the North Atlantic ocean exist, indicating an encouraging improvement with respect to the eddy energy distribution along both the North Atlantic current and the Azores current (Bryan and Smith, 1998; Smith et al., 2000). Coupling them with models of varying ecosystem complexity requires enormous computer resources, and the prospect of such high-resolution-coupled simulations is near at hand. Presently, global scale models do not have sufficient resolution to fully resolve details in high mesoscale activity regions. One possibility exists to model the large-scale dynamics and fully resolve the smaller-scale processes with the use of a nested model grid to gain increased spatial resolution in the region of frontal instabilities. Another possibility is to relate the effect of the frontal instabilities on the ecosystem to properties of the larger-scale fields through a parameterization of the tracer fluxes.

An isopycnally oriented, adiabatic parameterization for mesoscale tracer transport (Gent and McWilliams, 1990, Gent et al., 1995) has been tested with success in global coarse-resolution ocean models (Danabasoglu et al., 1994; England, 1995), yielding significant improvements in the global temperature distribution or in the localization of regions of deep convection to name a few.

Guided by baroclinic instability theory and calibrated against eddy-resolving calculations, Visbeck et al. (1997) proposed a form combining the best aspects of the Green (1970) and Gent and McWilliams approaches in which the transport by baroclinic eddies is parameterized in terms of an horizontal transfer coefficient k, given by $k = \alpha(f/\sqrt{\text{Ri}})\ l^2$, where l measures the width of the

baroclinic zone, α is a constant of proportionality (empirically found to be equal to 0.015), Ri is the Richardson number of the large-scale flow, and f the Coriolis parameter. The quantity $f/\sqrt{Ri}$ is a measure of the Eady growth rate, defined as the maximum growth rate of a disturbance to the flow during the growth of jet instabilities (Eady, 1949; Gill, 1982). Looking at biological tracer transport, Spall and Richards (2000b) tested Visbeck et al.'s formulation for the thickness diffusion (the eddy-induced transport velocity is related to a diffusion of isopycnic layer thickness; Gent and McWilliams, 1990), whereby the diffusion coefficients vary in space and time according to the large-scale fields based on the Eady growth rate. They also proposed and tested a somewhat modified Visbeck et al.'s parameterization in which the choice of the length scale l, during the initial stages of the frontal evolution, is not as large as the width of the jet. The evolution of the along front average quantities is found to be well represented in the parameterized model runs, and for the oligotrophic conditions at BATS in the summer months, the flux of a nitrate tracer from the parameterized runs also provides good estimates for the increase in new production associated with the jet instability (Spall and Richards, 2000b). As these authors point out, further testing of such parameterizations may yield a robust way to predict the effect of jet instabilities on the ecosystem without the need for computationally expensive, full eddy-resolving three-dimensional physical/ecosystem modelling.

In conclusion, the highly non-linear coupling between dynamics and biological activity at the mesoscale can be responsible for large variations in biogeochemical tracer distributions. Changes in plankton production and community structure due to the mesoscale features (meanders, filaments, eddies, fronts, etc.) can alter significantly the estimation of biological production and carbon export to the deep ocean. Patterns of variability may favor different ecological strategies. Mesoscale turbulence supports enhanced transport of biologically relevant material into and out of the surface layer because of asymmetric correlations between the velocity and bioscalar fields. The focus up to now is on the elevated new nutrient supply to the euphotic zone (though subducting organic matter export may also be of equal importance), which in turn can alter trophic interactions and community structure.

We are facing several major challenges to succeed in JGOFS synthesis. One is to be able to combine all the existing (physical, chemical, biological, bio-optical) data sets along with satellite information and state-of-the-art dynamical models using full four-dimensional assimilation schemes to progress in assessing the role of the oceanic mesoscale variability in the oceanic carbon cycle. This should lead us to answer: What data set is most informative about the quantities we are interested in? Do the data give us enough information to choose among candidate models? For instance, the ongoing Atlantic Meridional Transect (AMT) programme in the North Atlantic ocean along the 20°W transect offers a unique collection of core oceanographic measurements (key variables and process rates) from the polar to the tropical gyre domains (Aiken et al., 2000). A second challenge lies in the parameterization of vertical fluxes of nutrient. Changes in climate-driven physical forcing may impact on the frequency and nature of mesoscale activity in the open ocean, thereby affecting the ocean uptake of carbon. Such parameterization may offer the avenue to include the effect of mesoscale activity on the ecosystem in global scale bio-geochemical models for climate change predictions. A third challenge is to continuously improve our observational capabilities by developing new autonomous sensors and system technologies to be deployed on multi-disciplinary oceanic observatories, either on a Lagrangian or Eulerian mode.

Acknowledgements

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