

The relationship between the standing stock of deep-sea macrobenthos and surface production in the western North Atlantic

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Abstract

The relationship between surface production and benthic standing stock is fundamental to understanding biogeography in the deep sea. While much has been learned about the complex oceanographic processes involved in energy transfer to the benthos on local scales, the correspondence of overhead production to benthic community structure on regional scales remains poorly characterized. We compiled a database on the biomass and abundance of deep-sea macrobenthos in the western North Atlantic collected from 1961 to 1985. Using SeaWiFS satellite color imagery, we calculated POC from surface chlorophyll *a* concentrations (from 1997 to 2001), and estimated POC flux to the seafloor by using the empirically derived Pace et al. [1987. Primary production, new production and vertical flux in the eastern Pacific Ocean. *Nature* 325, 803–804] algorithm. The standing stock and surface production data are not concurrent, but their basic geographic trends at these very large spatial scales appear to be relatively stable over the time scales of measurement. Estimated POC flux at depth accounts for 62–67% of the variance ($P < 0.0001$) in benthic standing stock, suggesting that macroecological studies of the relationship between satellite-derived surface production and deep-sea community structure may be possible.

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1. Introduction

As perhaps the most indirect trophic connection in nature, the deep-sea benthos is fueled primarily by phytodetritus that originates as surface production and either sinks through the water column or is laterally advected. The entire process of pelagic–benthic coupling is exceedingly complex and still

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incompletely understood (Gage, 2003). It is clear that carbon flux decreases exponentially with depth (Suess, 1980; Pace et al., 1987; Berelson, 2001); this, in turn, is assumed to cause the well-known exponential decrease in benthic standing stock with depth (Rowe, 1983; Heip et al., 2001; Rex et al., 2006). This critical, but largely unquantified, assumption is often invoked to explain geographic patterns of community structure (reviewed by Levin et al., 2001; Stuart et al., 2003; McClain, 2004; Rex et al., 2005) and evolutionary divergence (Etter and Rex, 1990; Rex and Etter, 1998; McClain et al., 2004; Etter et al., 2005) within the deep sea. At a few sites in the ocean, long-term studies of satellite-derived primary production, sediment-trap measurements of carbon flux, sediment community oxygen consumption, and benthic standing stock have documented the major features of vertical energy transfer and its ultimate incorporation by the benthos (e.g., Smith et al., 2006). However, on the larger regional scales at which significant changes in benthic community structure are observed, little is known of the relationship between patterns of overhead production and the abundance of seafloor life. This relationship is vital to understanding biogeography in the deep sea.

It is theoretically possible to estimate the amount of organic material available to the benthos at depth. Recent ocean color imagery from the SeaWiFS satellite provides high-quality chlorophyll *a* concentration estimates (Rhea and Davis, 1997) and makes possible direct computation of surface POC (Loisel et al., 2002). Sediment trap studies (Berelson, 2001; Lutz et al., 2002) have generated empirical predictive models that take surface production as input and describe the rate at which particulate matter is re-mineralized as it descends through the water column. By combining satellite color data with these models, estimates of food supply to the benthos in terms of POC can be calculated and compared to measurements of benthic standing stock, at least on an annual or longer time scales. POC flux is expected to be a good predictor of standing stock because it is significantly related to benthic community energy demand although there are time lags involved (Smith and Kaufmann, 1999; Smith et al., 2002).

Despite all of the uncertainty about processes involved in pelagic–benthic coupling, Smith et al. (2006) recently were able to use satellite-derived surface chlorophyll concentrations to calculate export flux which was a significant predictor of

POC flux measured at sediment traps moored 50–600 m above the abyssal seafloor in the northeast Pacific. Sun et al. (2006) found a significant relationship between satellite-derived primary productivity and Holocene foraminiferan abundance at lower bathyal and abyssal depths at ocean-wide scales in the North Atlantic. Here, we examine the relationship between surface production and standing stock of the benthic macrofauna along a depth gradient at regional scales in the western North Atlantic.

2. Materials and methods

2.1. Benthic standing stock

We compiled benthic standing stock estimates from previous studies (Sanders et al., 1965; Rowe et al., 1974, 1982; Smith, 1978; Maciolek et al., 1987a, b) in the western North Atlantic (Fig. 1). The data represent the macrobenthos, primarily polychaetes, peracarid crustaceans, and molluscs retained on 300–420 μm sieves. The benthic samples cover depths extending from the shelf-slope transition down to the abyssal plain (200–5200 m), a latitudinal range of 33.1–41.3°N, and a longitudinal range of 65–73.8°W. Some samples in the Rowe et al. (1982) study were collected in Hudson Canyon. Standing stocks appeared to be elevated only at the canyon head (203–570 m), though no neighboring slope-face samples were available for comparison in that study. Standing stock data include both abundance (all studies) and wet-weight biomass (all except Maciolek et al., 1987a, b). In total, the benthic database includes 127 abundance estimates and 80 biomass estimates from samples collected between 1961 and 1985. The database, including sampling locality, type of gear, and sieve mesh size used is available as an online supplement.

2.2. Surface production

We acquired global 9 km resolution average monthly SeaWiFS satellite data in .hdf format through the University of New Hampshire Ocean Process Analysis Laboratory for September 1997 through December 2001. Each pixel represents 0.088° latitude by 0.088° longitude, or 9 km \times 9 km at the equator. In the western North Atlantic basin, each pixel is approximately a 9 km \times 6 km area. The data include the following relevant parameters: surface chlorophyll *a* concentrations ([Chl]), average

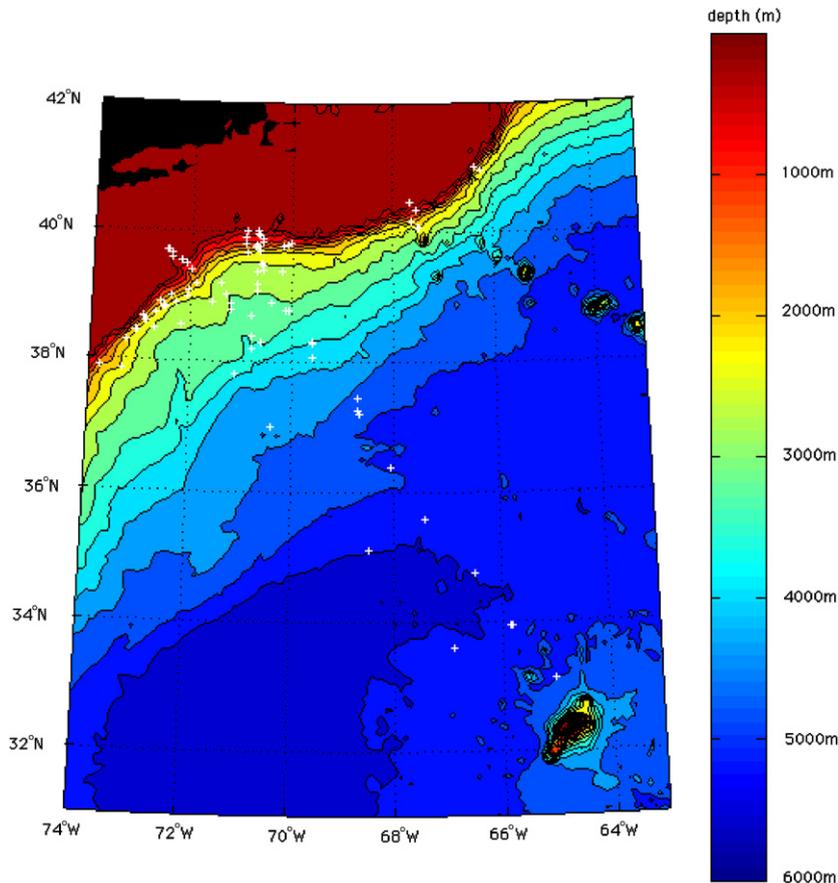


Fig. 1. Bathymetric map of the western North Atlantic. Contour lines are every 500 m, with an additional line at 200 m depth to mark the shelf boundary. Station locations for benthic standing-stock data are plotted as white + symbols.

attenuation coefficient for downwelling irradiance at 490 nm ($K_d(490)$), and normalized water-leaving radiance at 490 nm ($L_{wn}(490)$). POC was calculated by using the method of Loisel et al. (2002), though we have used a different relationship between POC and b_p (backscattering due to particles) based on Claustre et al. (1999). An explanation of the calculations is available in the online supplement.

The 4-year average of surface [Chl] over the western North Atlantic falls off rapidly with increasing distance to land (Fig. 2). The pattern of surface POC, not shown here, is similar. Fig. 2 demonstrates that most of the highly productive waters reside over the continental margin. The western North Atlantic experiences two plankton blooms over the course of the year, in the spring and late fall (Campbell and Aarup, 1992; Gregg, 2002). High productivity waters can extend beyond the shelf-slope margin during bloom periods (Campbell and Aarup, 1992; Ryan et al., 1999), and as episodic

events during periods of low productivity (Conte et al., 2003). Coastal stations exhibit much more variability over the course of a year than do deep-water stations. The nature of the spring bloom is discussed at length by Follows and Dutkiewicz (2002).

2.3. Scaling

Given the spatial and temporal variations in surface production and dispersal of export flux by currents, a fairly large spatial domain must contribute organic carbon to a local benthic site. Deuser et al. (1990) proposed that this domain be conceptualized as a statistical funnel. The ocean surface supplying the funnel with export flux is termed its catchment area. Sizes of catchment areas are still poorly characterized but models of statistical funnels suggest dimensions approaching 100 km (Siegel and Deuser, 1997; Siegel and

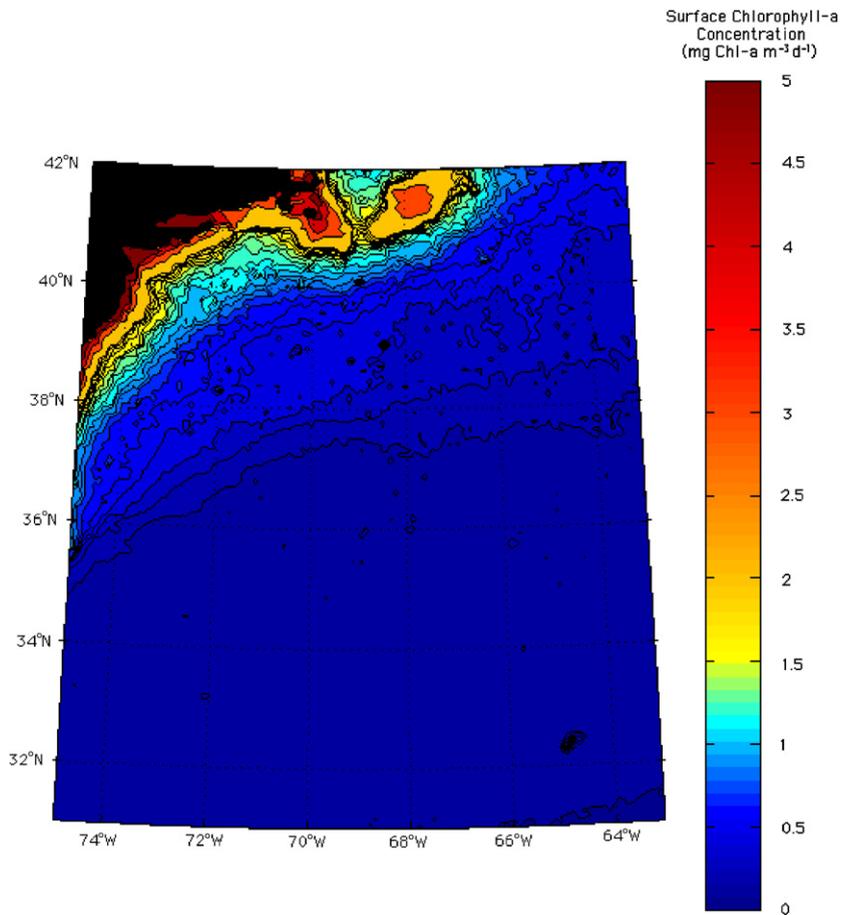


Fig. 2. Contour map of average daily surface chlorophyll *a* concentrations in the western North Atlantic over a 4-year period from 1998 through 2001. Concentrations are high nearshore, and decrease with increasing distance from land. POC contour map (not shown) is qualitatively similar in pattern, and spans almost 3 orders of magnitude from approximately 30–700 mg C m⁻³ d⁻¹.

Armstrong, 2002). The shapes, sizes, and locations of catchment areas may be temporally dynamic (Waniek et al., 2005).

To estimate carbon flux to each benthic station, we defined potential catchment areas by constructing circles of varying diameters ($d = 1, 3, 5, 7$ pixels) centered above each station at the surface. Pixels were included in the circle if the center of the pixel fell within the radius ($r = d/2$). Spatial scales examined here range from ~ 54 km² for one pixel diameter circles to ~ 1998 km² for seven pixel circles. All pixels within this circle were averaged to obtain a single value for initial export flux into the water column above each station. In a preliminary examination, we evaluated scales up to 31 pixel diameter circles ($\sim 41\,000$ km²), comparable to those used by Deuser et al. (1990) to identify the primary geographic position of catchment areas relative to

moored sediment traps. Visual inspection revealed no noticeable differences between the seven pixel diameter and larger scales in average surface [Chl] per pixel.

Clearly it would be preferable to have a benthic database that represented contemporaneous sampling and fully standardized sampling methods. Both gear type (Gage, 1975; Hughes and Gage, 2004) and sieve mesh size (Gage et al., 2002; Gage and Bett, 2005) can affect sampling efficiency for the deep-sea macrobenthos. However, these variables can also be controlled for by partial regression analysis. In our analysis of biomass and abundance, we first tested for the statistically independent effects of sampling date, sampling gear, and sieve mesh size. The effects of longitude and latitude also were examined because we are primarily interested in depth-related phenomena (Rex et al., 2006).

The residuals of biomass and abundance, with methodological and geographic variables held constant, were used as the response variables to regress against estimated POC flux at depth as the explanatory variable. To recapture the actual measured scales of biomass and abundance, we added the y -intercepts from the multiple regressions and the mean of each of the independent variables.

2.4. Benthic food supply

Several studies have proposed relationships between depth and sinking particulate organic matter based on sediment trap data (Suess, 1980; Pace et al., 1987; Deuser et al., 1990). We used the algorithm developed by Pace et al. (1987), which provides the most accurate predictions of material at depth among the algorithms tested by Berelson (2001). We applied the Pace algorithm,

$$\text{POC}_z = 3.523 \times z^{-0.734} \times \text{POC}_0,$$

to surface energy estimates for each station to calculate available energy at the sea floor. The variable z in the algorithm is depth, and POC_z is the particulate organic content at depth z . POC_0 is POC at depth 0, the surface. The original Pace algorithm used primary productivity rather than POC_0 as the independent variable. This raises the possibility that the tuning parameters of the equation may be inappropriate. We also performed the analysis by using Pace-transformed estimated surface chlorophyll a concentration. The predictive values of chlorophyll a concentration and POC were quite similar ($r^2 = 0.630$ vs 0.617 and 0.652 vs 0.662 , respectively, for benthic biomass and abundance). The relationships are linear as they are with POC. It seems reasonable to assume that POC decreases exponentially with depth. However, since constants in the algorithm have not been empirically fitted for POC, this could be a potential source of error.

3. Results and discussion

Testing for the independent influence of sampling methods and geographic position on abundance and biomass required two separate analyses, either with gear or with sieve size included, since sieve size did not have sufficient replication within gear categories. For tests including POC flux, sieve size had a significant effect on abundance ($F = 16.11$, $P < 0.0001$). Gear used as a nominal variable also had a significant effect on abundance ($F = 3.24$,

$P < 0.01$), but multiple comparison tests failed to find differences among gear types (anchor dredge, Berge Ekman boxcore, UNSEL boxcore, Ekman grab, and van Veen grab). There were no independent effects of gear, sieve size, date, or geographic position on biomass. In general, the effects of methodologies and geographic variables were very subordinate to the independent influence of POC flux ($F = 82.58 - 251.41$, $P < 0.0001$). POC flux was regressed against biomass and abundance with sieve size, date of collection, latitude, and longitude held constant for consistency.

A pairwise comparison of 1–7 pixel diameter spatial scales showed highly significant correlations in the order of sites by surface [Chl] (Spearman rank order correlations $r_s = 0.94 - 0.99$, $P < 0.0001$). Thus, regardless of the spatial scale, the pattern of variation in surface production across stations is very similar. Smith et al. (2006) compared three potential catchment areas to predict the relationship between export flux calculated from satellite-derived chlorophyll concentration and POC flux measured at a moored sediment trap; these were 50 and 100 km radius circles and a 200–600 km oval oriented parallel to the current, and centered above the sediment trap. Export flux from all three catchment areas provided nearly identical correlations with measured POC flux, though the 50 km circle provided the shortest time lag between export flux and flux measured at depth. In the following analysis, we use seven pixel diameter catchment areas because r_s values tended to increase slightly between larger scales, and the general current consensus that larger catchment areas are more relevant (Smith et al., 2006).

Similarly, pairwise comparisons between yearly averages of [Chl] at the same spatial scale were highly significant ($r_s = 0.94 - 0.98$, $P < 0.0001$). The variance in biomass and abundance accounted for by estimated POC flux at depth is high and very similar among years ($r^2 = 0.605 - 0.622$ for biomass, and $r^2 = 0.634 - 0.684$ for abundance, $P < 0.0001$). In our analysis below, we use 4-year averages of estimated flux to the benthos. We stress that we are not attempting to identify the appropriate catchment area for a single site such as a moored sediment trap. Rather we relate two large-scale ecological patterns, benthic standing stock and surface production at what seem to be reasonably pertinent scales of time and space.

Macrobenthic biomass and abundance are plotted against Pace-transformed POC in Figs. 3

and 4. The relationships between POC flux and standing stock are linear. Pace-transformed POC explains 62% of the variance in

biomass; and 67% of the variance in abundance ($P < 0.0001$).

Correlation does not imply causality. However, standing stock and other measures of benthic community structure can now be examined as a function of a directly relevant environmental variable, rather than a geographic axis (depth) that is assumed to be a surrogate for food supply. Given the complexity of pelagic–benthic coupling, and the huge spatiotemporal variability of surface production and downward flux of POC, it is remarkable that estimates of food supply to the benthos based on overhead production and transfer through the water column can explain most of the variation in benthic standing stock. This suggests that it might be possible to predict macroecological patterns in the deep sea with reasonable accuracy from satellite-derived patterns of surface production, at least on large scales. This would allow much more explicit tests of biodiversity theories such as the relationship between species diversity and productivity (Levin et al., 2001; Stuart et al., 2003; Rex et al., 2005).

While there is a significant and convincing positive relationship between estimated carbon flux and standing stock (Figs. 3 and 4), the data are noisy. The relationships are anchored by tight clusters of points representing deep samples with

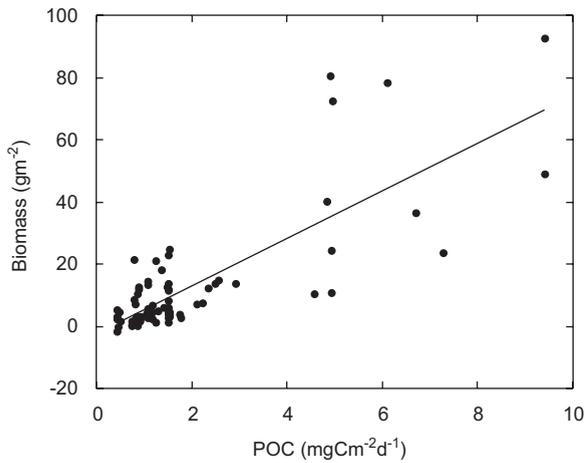


Fig. 3. The relationship between estimated POC flux and wet-weight biomass of the deep-sea macrobenthos in the western North Atlantic. The effects on biomass of sieve size, date of collection, latitude, and longitude are held constant by partial regression. This accounts for some slightly negative values of biomass. See Fig. 1 for a map of the deep-sea sampling stations. Regression equation and statistics for relationships are: $\text{biomass} = -3.175 + 7.659 \text{ POC}$, $N = 80$, $F = 129.323$, $P < 0.0001$, $r^2 = 0.624$.

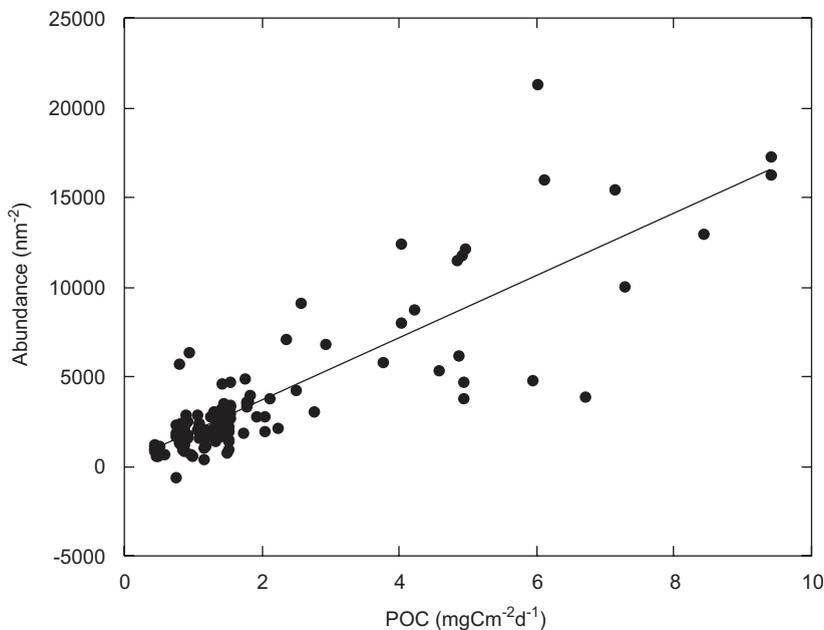


Fig. 4. The relationship between estimated POC flux and abundance of the deep-sea macrobenthos in the western North Atlantic. The effects on abundance of sieve size, date of collection, latitude, and longitude are held constant by partial regression. This accounts for some slightly negative values of abundance. See Fig. 1 for a map of deep-sea sampling stations. Regression equation and statistics for the relationship are: $\text{abundance} = 250.522 + 1751.934 \text{ POC}$, $N = 127$, $F = 255.731$, $P < 0.0001$, $r^2 = 0.672$.

low standing stock, and low overhead production. Higher values on the continental margin show considerably more variation, possibly because the bathyal region is a more dynamic environment where downslope transport and lateral advection create a more heterogeneous trophic regime, and one that may not primarily represent vertical flux. In Fig. 3, the biomass values corresponding to the highest POC values ($>4 \text{ mg C m}^{-2} \text{ d}^{-1}$) are all from the head of Hudson Canyon (Rowe et al., 1982). Since there are no comparable slope-face data available, it is unclear what effect the canyon environment might have. For abundance (Fig. 4), however, canyon and slope-face data are completely mixed ($>4 \text{ mg C m}^{-2} \text{ d}^{-1}$) indicating no canyon effect. In fact, the highest abundance value is from the slope face. More bathyal data are needed to better characterize the relationships shown in Figs. 3 and 4, especially at upper slope depths.

The 30–40% of the variation in standing stock that is not accounted for by estimated POC flux at depth suggests that surface–benthic coupling is not tight, at least on the scales examined. Presumably this residual variance reflects other biotic and abiotic factors that affect connectivity between surface and benthic systems, as well as measurement error and shortcomings of our analytical approach. Examples of other paths of nutrient flow, not represented in the Pace algorithm, include downslope transport (Hecker, 1990), lateral advection by deep currents and mesoscale eddies (Herman et al., 2001; Conte et al., 2003), off-shelf movement (Rowe et al., 1994), and riverine input (Schlunz and Schneider, 2000; Hansell et al., 2004). Large rapidly sinking parcels of plant and animal material and their subsequent redistribution by benthic herbivores and scavengers (Priede et al., 1991) introduce additional patchy sources of food to the benthos (Wolff, 1979; Stockton and DeLaca, 1982; Smith and Baco, 2003). The vertical movement and trophic role of dissolved organic carbon, almost certainly significant to benthic bacteria (Deming and Yager, 1992), and possibly to metazoans as well, also remain poorly quantified. Empirically derived flux–depth relationships vary regionally (Lutz et al., 2002); therefore, the single Pace algorithm used here may not be appropriate throughout the large area considered (Fig. 1). The same could be said for using a single catchment area and temporal scale. Bottom-related processes such as carbon cycling in the benthic boundary layer (Smith, 1992), diagenesis within the sediment

community (Smith and Rabouille, 2002), and carbon turnover by the benthos (Witte et al., 2003) probably all vary significantly with depth, and could affect standing stock.

We also hasten to point out that Pace-transformed POC is not completely independent of depth since depth is a variable in the equation. In fact, the predictive value of depth for abundance and biomass ($r^2 = 0.73$ and 0.59 , respectively) is very similar to POC flux at depth, though the form of the relationship is curvilinear rather than linear. A similar result was reported by Watts et al. (1992) using Coastal Zone Color Scanner Satellite imagery. Significant relationships were found between surface pigment biomass and macrobenthic standing stock; but these relationships either collapsed or became weakly significant with the effect of depth removed by partial correlation. Thus, while Pace-transformed POC is a more relevant biological variable than depth per se, it adds no additional predictive value.

The most obvious weakness of our analysis is that data on surface production and benthic standing stock are not concurrent. We assume that the general spatial pattern of surface production observed in 1997–2001 is at least similar to that of 1961–1985 when the benthic samples were collected. The benthic data span two decades and are separated from the satellite data by more than a decade. There is no contemporary dataset that includes both large-scale benthic sampling programs and surface production that we are aware of. Much of our understanding of large-scale biogeography and macroecology in terrestrial and coastal systems is founded on comparing recent climate patterns to data on community structure from long-term biotic surveys that often represent decades to centuries of collecting. Our analysis seems like a useful preliminary step to explore the relationship between standing stock and surface production despite all of the uncertainties involved. New deep-sea sampling programs will be able to refine this relationship by simultaneously collecting both benthic data and satellite data on surface production.

The potential effects of the temporal differences in the data are hard to evaluate, but may not be severe. There is no independent effect of collecting time on standing stock when POC flux, geographic and sampling variables are held constant ($F = 0.16$ – 0.94 , $P = 0.33$ – 0.68), suggesting that standing stock remained stable over the 25-year span of sampling. Intensive precision sampling of

the macrobenthos in the bathyal western North Atlantic failed to detect seasonal or interannual signals in community makeup over a 2-year period (Maciolek et al., 1987a, b; Grassle and Maciolek, 1992). Sediment oxygen demand in the abyssal western North Atlantic also appears to be stable on interannual scales (Sayles et al., 1994). Macrofauna can rapidly ingest phytodetritus (Witte et al., 2003), and the reproductive cycles of some species may be linked to seasonal phytodetritus accumulation (Tyler, 1988; Gage, 1992). However, depositional events are not followed by changes in standing stock of the macrofauna as a whole (Pfannkuche, 1993; Galéron et al., 2001), though one important taxon, the polychaetes, can show increased density 9–18 months after deposition (Drazen et al., 1998; Galéron et al., 2001). So, while bacteria and some meiofaunal elements exhibit a rapid opportunistic response to seasonal phytodetrital settlement on the bottom (Gooday, 2002), the overall macrofaunal response in terms of population growth seems to be very muted, and delayed on the order of a year in taxa that do respond.

Nonetheless, it is also clear that significant seasonal, interannual, and decadal-scale changes of food supply to the benthos do occur, and that major climate shifts are associated with marked changes in the abundance and species composition of the epibenthic megafauna (Billett et al., 2001; Ruhl and Smith, 2004; Smith et al., 2006). Even though seasonal or episodic phytodetrital accumulations on the seafloor appear to be rapidly exploited by the mobile megafauna, it would be surprising if there were no effects on the macrofauna, even though evidence for this remains elusive. It seems very unlikely that climatically forced changes in surface production would fundamentally change the general positive relationship between estimated carbon flux and macrobenthic standing stock (Figs. 3 and 4). A recent synthesis of satellite-derived estimates of surface production from 1979 to 2002 found a global increase in average chlorophyll concentration, but this was primarily due to increases in the tropics (Antoine et al., 2005). The temperate North Atlantic remained relatively stable. Long-term changes in the level of surface production should affect the elevation of the regressions, just as observed in comparisons of standing stock–depth relationships among oligotrophic, mesotrophic, and eutrophic basins (cf. Rowe, 1971; Tselepidis and Eleftheriou, 1992). Shifts in the onshore–offshore gradient of

productivity should alter the slope of the standing stock–depth regressions for the same reason that standing stock–depth patterns are modulated by variation in local food supply associated with sediment depocenters (Blake and Hilbig, 1994), concentrating topographic features (Danovaro et al., 2003), and oxygen minimum zones (Levin, 2003).

We were unable to detect significant scaling effects among four separate years or by size of the catchment areas used to predict standing stock. Given the apparent temporal constancy of benthic standing stock, the scale invariance may mean that biomass and abundance represent nutrient input averaged over large scales of time and space. However, it is possible that longer time scales, and simulations using a broader array of catchment size, shape, and position relative to benthic stations are more appropriate. Also, while we feel that it is realistic to conduct a preliminary analysis of the general relationship between surface production and benthic standing stock at large geographic scales using data that are not concurrent, any attempt to identify the specific scales involved using temporally disjunct data is clearly a much more tenuous exercise. It may not be practical to design long-term large-scale benthic sampling programs that can effectively partition the variance in benthic standing stock between temporal and spatial variations in surface production; that is, a controlled sampling design in which both surface and benthic measurements are taken on scales that capture the full range of variation in both systems. Relevant scales of time and space can be assessed much more precisely by long-term studies that simultaneously measure surface production, POC flux and benthic processes (Smith et al., 2006). Given the logistical constraints of deep-sea research, an understanding of macroecological patterns will ultimately require both integrated experimental studies of carbon flux at specific sites, and comparative studies that document large-scale biogeographic patterns in both surface production and benthic community structure.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version, at doi: [10.1016/j.dsr.2007.04.011](https://doi.org/10.1016/j.dsr.2007.04.011)

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