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On the relationships between primary, net community, and export production in subtropical gyres

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Abstract

It has been proposed that net primary production (NPP), net community production (NCP), particulate organic carbon export (Φ_{POC}) and the relationships among them are governed by local environmental conditions that favor either a microbially dominated assemblage leading to a regeneration loop (low ratio of Φ_{POC} to NPP) or a system dominated by large plankton with export pathway characteristics (high ratio of Φ_{POC} to NPP). We analyze more than 10 years of data from two subtropical time-series stations (Hawaii Ocean Times-series (HOT) in the North Pacific, and Bermuda Atlantic Time-Series (BATS) in the North Atlantic) in order to investigate this regeneration loop versus export pathway hypothesis and in particular to test the idea that the switch between the two is controlled by enhanced input of nutrients. In the decadal long-term mean, the relationships between NPP, Φ_{POC} and NCP, which we take here as a proxy for export production, reveal export pathway characteristics at BATS, while HOT is dominated by the regeneration loop. This difference is consistent with the stronger seasonal forcing at BATS and the resulting higher new nutrient input. However, these characteristics are only valid for parts of the year. Especially at BATS, the export pathway exists only in spring and the system reverts to a regeneration loop in summer and fall. This is consistent with our hypothesis given the strong summer-time stratification and the resulting low levels of new nutrient input. On interannual time-scales, we find little evidence for statistically significant alterations of the long-term mean characteristics, a finding we ascribe to a combination of limited magnitude of forcing, length of the data records, and possibly an inherent lack of predictability. A comparison of our results for the ratio between NCP and NPP (e-ratio) and the ratio between Φ_{POC} and NPP (pe-ratio) with those predicted by the models of Laws et al. [Temperature effects on export production in the open ocean. Global Biogeochemical Cycles 14(4), 1231–1246] and Dunne et al. [Empirical and mechanistic models for particle export ratio. Global Biogeochemical Cycles 19, GB4026] respectively, show reasonable agreement for the long-term mean, but these models fail to capture the observed interannual variability in these ratios.
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1. Introduction

Alterations in the oceanic phytoplankton community structure and productivity affect the ocean carbon cycle and potentially also atmospheric CO_2 and climate (Sarmiento et al., 1998; Bopp et al., 2001; Chavez et al., 2003). Changing species composition can modify the nutrient and carbon reservoirs in the surface ocean and alter the pathways and amounts of organic matter exported out of the euphotic zone (Legendre and Le Fèvre, 1989; Karl, 1999; Cullen et al., 2002). Such variations can change the amount of carbon that is stored in subsurface layers of the oceans and may alter the exchange of CO_2 across the air–sea interface, as well as influence higher trophic levels and the oceanic food web. We focus here on a comparison of the ecosystem structure and its impact on the relationships between primary, net community and export production at two contrasting sites in the subtropical gyres of the North Atlantic and the North Pacific Oceans. Our particular goal is to test the hypothesis that variations in nutrient supply resulting primarily from variations in physical forcing will lead to predictable changes in phytoplankton community structure and the relationships between the different measures of production.

Production of organic matter in the surface ocean is governed by the availability of light and nutrients, while the organic matter export to depth depends on the effectiveness of remineralization processes throughout the water column. Net primary production (NPP) describes the net fixation of inorganic carbon by autotrophic organisms, i.e. the difference between gross primary production (GPP) and autotrophic respiration. Part of this organic material is respired locally. The difference between NPP and this heterotrophic respiration is termed net community production (NCP) (Williams, 1993). In steady-state and when averaged over sufficient length scales, NCP can be regarded as being numerically equivalent to export production, i.e. the flux of organic carbon out of the euphotic zone. This export takes place either in the form of particulate organic matter (POM), which tends to be exported vertically by sinking, in the form of dissolved organic matter (DOM), which can be exported both laterally and vertically, or via active zooplankton migration and excretion (Steinberg et al., 2000), respiration, molting or death at depth.

The vast subtropical gyres of the ocean tend to be a low-nutrient, low-productivity regime, which favors the "regeneration loop" (Sarmiento and Gruber, 2006; Cullen et al., 2002). This concept refers to a picophytoplankton based ecosystem with most production fueled by recycled nutrients, with low export and a low f-ratio, the ratio of new production to NPP (Dugdale and Goering, 1967; Eppley and Peterson, 1979). In these food-limited regimes, picophytoplanktonic organisms are generally grazed effectively by small nano- and microzooplankton preventing strong accumulation of picophytoplankton. The net effect of this intense grazing and coupled heterotrophic bacterial utilization of locally produced DOM (Azam et al., 1983; Azam, 1998) is a nearly quantitative remineralization of nitrogen and phosphorus. Export in this regeneration loop occurs primarily by two processes: Lateral and downward transport of DOM and sinking of POM produced by zooplankton.

In more nutrient-rich conditions, the regeneration loop can be augmented or even dominated by the "export pathway". In export pathway dominated systems, we additionally find large phytoplankton species that are grazed by large zooplankton species, and export occurs primarily in the form of large and rapidly sinking POM. This combined ecosystem is generally based on the concurrent existence of diatoms, picophytoplankton and heterotrophic bacteria, and is characterized by a high f-ratio. In these conditions, a combination of high nutrient supply (compared to regeneration loop-dominated systems), light availability and an effective biological pump (that removes organic material and the incorporated nutrients) leads to a low-nutrient and medium- to high-productivity regime, in which the export pathway is active during times with increased nutrient supply.

This concept, whose roots can be traced back to the classical work of Margalef (1968), is a powerful framework, but it is not complete. For example, it does not explicitly account for the role of nitrogen fixers, which have been shown to be an important source of nitrogen for upper ocean ecosystems in the subtropical gyres (Karl et al., 1997; Capone et al., 1997, 2005). Their contribution to the variability of ecosystems could be incorporated into this concept as a modification of the export pathway. Scharek et al. (1999), for example, pointed out that the largest export pulse during 1994/1995 measured at Sta. ALOHA in the North Pacific appeared to be supported by nitrogen fixation during well-stratified conditions.

The goal of this study is to determine which environmental conditions favor the export pathway over the regeneration loop. Our working hypothesis, based largely on extant conceptual models, is that higher inputs of nutrients as a result, for example, of deeper mixed layers, will lead to enhanced rates of NPP, favoring large phytoplankton species, intensified export of particulate organic matter and, hence, the export pathway. A secondary control might exist in the form of temperature, assuming that lower temperatures will slow down heterotrophic processes more that they do autotrophic ones, also leading to an intensified export (Laws et al., 2000). Inherent in our hypothesis is the assumption that the structure and dynamics of the upper ocean ecosystem respond in a predictable manner to environmental forcing.

To test this working hypothesis, we investigate the relationships between NPP (as determined by the in situ ^{14}C method), NCP, and Φ_{POC} and their connections to phytoplankton community structure as reflected in pigment data on the basis of two long time-series records in the subtropical gyres of the North Atlantic and North Pacific, respectively. We will address the following questions: How do NPP, NCP and Φ_{POC} relate to each other and can we understand the differences between the sites and the temporal variations at each site in terms of a deterministic response to physical forcing? We investigate long-term mean values, mean seasonal cycles and time-series of annual means, i.e. interannual variations of the annual means. We focus here on annual and seasonal means in order to average out the impact of the temporal decoupling of production and export (Buesseler, 1998). An additional advantage of this approach is that it is less sensitive to episodic events (e.g. see Karl et al., 2003b).

Ratios have been defined to express the relationships between production and export. The e-ratio describes the ratio between export production and NPP (Laws et al., 2000). In steady-state and when averaged over sufficiently large spatial scales, new production can be equated to export production (see Plattner et al., 2005 for a discussion of limits). Under these conditions, the e-ratio is numerically identical to the f-ratio. As a consequence, several investigators have combined estimates of the e- and the f-ratios and refer to these estimates as the ef-ratio (Laws et al., 2000). Dunne et al. (2005) introduced the term "pe-ratio" to refer to the fraction of NPP that is exported as particulate matter. Consequently, one can refer to the fraction of export that occurs in form of sinking particulate matter as the p-ratio (Brix et al., 2004).

Based on our hypothesis, Fig. 1 shows how we expect NPP, NCP, and Φ_{POC} to be related to each other, and how this impacts the different ratios. For the e- and the pe-ratio (Fig. 1A and C), we expect these ratios to increase with increasing NPP, i.e. we expect the observations to lie along trends that cross lines of equal ratios. This expectation is a direct consequence of our postulating an increasing contribution from the export pathway when NPP increases, leading to higher export relative to NPP (higher e-ratio) and a higher contribution of particle export (higher pe-ratio). Our hypothesis is less specific with regard to the p-ratio, but we also expect a somewhat higher contribution of particles to total export, i.e. higher p-ratio, with increasing NCP (export).

Diagnostic, empirical and mechanistic models have been developed to investigate variations of these ratios in relationship to physical and ecological quantities. In the model of Laws et al. (2000), the ef-ratio is analyzed as a function of temperature and NPP. Dunne et al. (2005) describe the pe-ratio as a function of temperature, NPP and depth of the euphotic zone. In both models the respective ratios rise with decreasing temperature and increasing production, similar to the conceptual model shown in Fig. 1. We apply these models in our investigation and test their validity.

The subtropical gyres are ideal testbeds for our investigations thanks to the establishment of two long-term upper ocean time-series of carbon, nutrients and biological parameters. These sites have been set up as part of the US Joint Ocean Global Flux Study (JGOFS) program: one near Bermuda (Bermuda Atlantic Time-Series, BATS), building on the long running time-series from Hydrostation "S" (Michaels and Knap, 1996), and one near Hawaii (Hawaii Ocean Time-series program, HOT (Karl and Lukas, 1996) with the measurements taken at Sta. ALOHA). Quasi-monthly sampling started in 1988 at both sites and continues to the present (Lomas et al., 2002). Ideally, one would want to extend our analysis to other sites spanning a wider range of environmental conditions, but, to our knowledge, there are no other time-series available that include estimates of all required parameters over an extended period of time. Especially, there are very few places that have reported estimates of NCP.

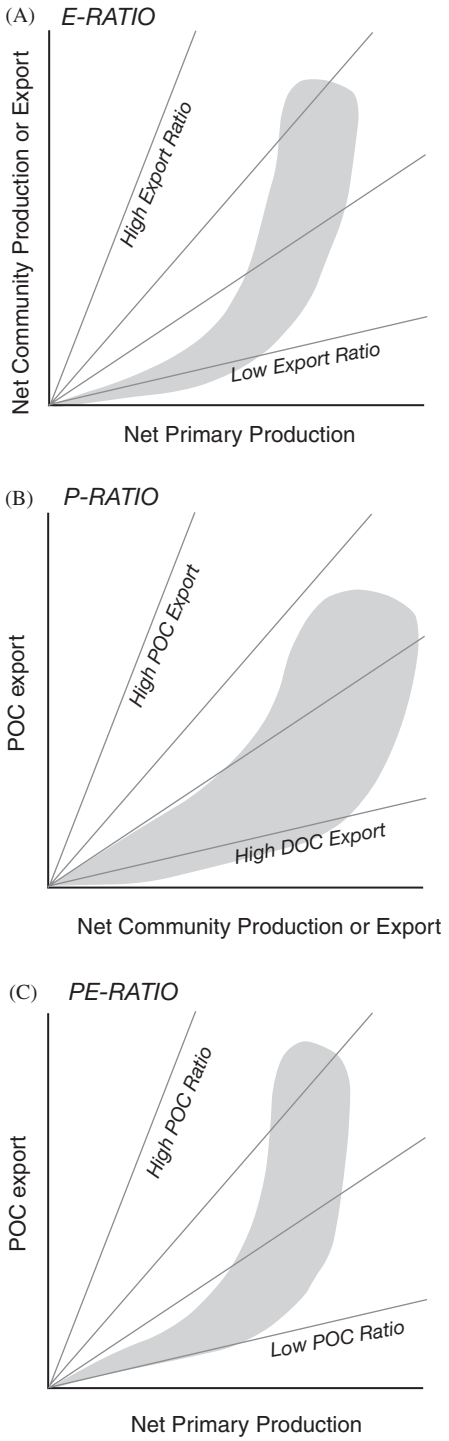


Fig. 1. Plots of the expected relationships between NPP, NCP, and particulate organic carbon (POC) export according to our conceptual model. The thin lines in each panel denote lines of constant ratios, i.e. of the e-ratio in (A), p-ratio in (B), and pe-ratio in (C). The gray shades indicate the trends expected based on our hypothesis with regard to the relative roles of the regeneration loop versus the export pathway as a function of increasing productivity (see text for details).

2. Data sets

The majority of the data employed in this study are from the HOT and BATS core measurement program for the years 1989 until 2000 (Lukas and Karl, 1999 for HOT and Steinberg et al., 2001 for BATS, data available under http://hahana.soest.hawaii.edu/hot/hot-dogs/, and http://bats.bbsr.edu/, respectively). We employ the in situ ^{14}C incubation measurements (Knap et al., 1993) undertaken at both sites from dawn to dusk as estimates for NPP. Although this technique has a number of unresolved methodological problems (Marra, 2002), it is widely used as measure for NPP. It should be noted that ^{14}C incubation, performed from dawn to dusk, does not include the contribution of photoautotrophic respiration at night, which, however, is likely to have a minor effect on NPP. We vertically integrated the measurements taken at discrete depths over the top 150 m for both stations. Unfortunately, such data are available for the HOT site only until 2000 (from 2001 onward the deepest ^{14}C incubations were performed at 125 m). We nevertheless choose 150 m as the lower boundary because it coincides with the depth of the shallowest sediment traps. It also corresponds to the depth of the euphotic zone, i.e. the depth at which photosynthesis is balanced by autotrophic respiration for Sta. ALOHA (Laws et al., 2000), while the base of the euphotic zone at BATS is somewhat shallower (approximately 100 m, Steinberg et al., 2001). However, the contribution of production between this depth and 150 m to the integrated value over the entire 150 m is small (mean about 5%) and therefore neglected.

The export flux, Φ_{POC}, is based on the analysis of particulate organic matter collected in free-drifting sediment trap arrays (Knauer et al., 1979) deployed at approximately 150 m depth for between two to three days during each cruise. Sediment trap design, collection and processing methods are described in detail by Karl et al. (1996) for HOT and in the "Methods Manual" for BATS available under http://bats.bbsr.edu/docs/methods/report_methods.pdf. There are a number of unresolved questions with regard to the calibration, accuracy and precision of such shallow sediment trap data, concerning, e.g. removal of swimmers (zooplankton), hydrodynamic biases, difficulties in separating particulate inorganic carbon from POC, and others (Michaels et al., 1994; Buesseler, 1998). Sediment traps are, however, one of the few tools available for

estimating the flux of sinking particles in the ocean and the only estimate available here.

NCP was estimated on the basis of a diagnostic box model approach (Gruber et al., 1998) that takes advantage of concurrent $\delta^{13}C$ and dissolved inorganic carbon (DIC) data, which, together with measurements of additional chemical and physical parameters, allow a quantitative derivation of all major processes that contribute to the upper ocean carbon cycle. The contributions of air–sea gas exchange, vertical diffusion and entrainment to the $\delta^{13}C$ and DIC budget of the mixed layer are estimated on the basis of observations and well established parameterizations, while horizontal transport and NCP are diagnosed on the basis of budget constraints. Since NCP is derived from the temporal evolution of the measured DIC and $\delta^{13}C$, it is by design a time-integrative measure of this production and therefore fundamentally different from the point measurements of NPP and Φ_{POC}. As the model integrates measurements by using harmonic and spline fits of the actual data, NCP is well constrained for seasonal to annual time scales, but not at shorter time scales. As a result, the model estimated NCP cannot be compared directly to point measurements of NCP such as those of Williams et al. (2004) for Sta. ALOHA on the basis of an O_2 flux technique. The modeling approach to estimate NCP was employed by Gruber et al. (1998, 2002) for BATS, and Keeling et al. (2004) and Brix et al. (2004) for Sta. ALOHA (as well as Quay and Stutsman, 2003 with a slightly different model). We used the NCP values for BATS from Gruber et al. (2002) and Sta. ALOHA from Brix et al. (2004). The carbon-13 constrained estimates of NCP for the mixed layer were extrapolated to the entire euphotic zone using information about the vertical profile of NPP and the mixed-layer depth (MLD). For each four-month time interval of the respective time-series site, we determined the fraction of NPP that takes place within the mixed layer and then assumed that the depth dependence of NCP scales with the depth dependence of NPP, i.e. we divided mixed-layer NCP by the NPP-based mixed-layer fraction. Note that the resulting values for the euphotic zone NCP are different than those reported by Brix et al. (2004), as the latter used a constant fraction of 0.8, while we use here a time-varying fraction. This need for extrapolation increases the uncertainty of the euphotic zone estimates of NCP.

Phytoplankton pigment concentrations were determined by high-performance liquid chromatography (HPLC) for Stations BATS and ALOHA (see Bidigare et al., 1991; Steinberg et al., 2001; Lomas and Bates, 2004 and the data web sites). Chlorophyll-*a* (Chl-*a*) is the primary pigment for all prokaryotic and eukaryotic photoautotrophs. We therefore regard Chl-*a* as a proxy for phytoplankton biomass, recognizing that we thereby neglect a potential bias due to variations in the Chl-*a* to carbon (biomass) ratio. Both stations have a deep chlorophyll maximum that lies deeper than the NPP maximum, a clear indication of a high Chl-*a* to carbon ratio at the chlorophyll maximum. To estimate the influence these uncertainties could have on our calculations we estimated depth-integrated chlorophyll for the top 20, 80, and 150 m by first binning all casts of one station occupation into 10 m deep bins and then integrating the bins vertically. Values for bins without measurements were estimated by linear interpolation of next neighbors. Although most of the measurements have been taken at distinct depths over most of the time-series, we choose to use bins to account for the few cases that departed from that rule. The time-series of the three different depth-integrated values at both stations are significantly correlated with each other, with smallest correlation values of $r = +0.65$ for the correlation of the upper 20 m with the upper 150 m for the entire time-series at HOT. The correlations are higher ($r > +0.80$) for annual mean values. Given these high correlations, which suggest that variations in the Chl-*a* to carbon ratio are secondary in importance to changes in biomass, we choose to use the integral over the entire euphotic zone (defined for this purpose as the top 150 m) for all further computations.

To investigate changes in community structure, we analyze two other HPLC pigments: Chlorophyll-b (Chl-*b*) and fucoxanthin (*Fuco*). Chl-*b* can be regarded as an estimate of the abundance of the picophytoplankton *Prochlorococcus*, and *Fuco* is regularly used as a diatom marker (Karl et al., 2001). For a strict analysis we would need to consider that other species besides *Prochlorococcus* contain Chl-*b* (Letelier et al., 1993), and in order to determine the diatom fraction, *Fuco* would need to be corrected for the presence of 19′-*butanoyloxyfucozanthin* and 19′-*hexanoyloxyfucoxanthin* (Lomas and Bates, 2004). We abstained from calculating these corrections, as the pigment analysis in this context is intended to search for indications of community changes without the need for an accurate quantification. As done for Chl-*a*,

these other pigment data were also vertically integrated to 150 m. The respective fractions of *Prochlorococcus* and diatoms relative to the total biomass, i.e. the Chl-*b*/Chl-*a* and *Fuco*/Chl-*a* ratios, were computed from seasonal means of the pigment data. We use high *Fuco*/Chl-*a* ratios as an indication of a diatom enriched assemblage and high Chl-*b*/Chl-*a* for a *Prochlorococcus*-enriched assemblage in the habitats under consideration.

MLD were estimated from vertical profiles of potential density, σ_Θ, computed from CTD temperatures and salinities applying the temperature dependent density criterion of Sprintall and Tomczak (1992):

$$\sigma_{\Theta,mld} = \sigma_{\Theta,0} + \Delta T \frac{\partial \sigma_\Theta}{\partial T}, \quad (1)$$

where $\sigma_{\Theta,0}$ is the surface potential density, $\partial\sigma_\Theta/\partial T$ is the thermal expansion coefficient, and using a temperature difference, ΔT, of 0.5 °C. Wind speed data used are monthly means from the National Center for Environmental Prediction (NCEP) Reanalysis data provided by the NOAA-CIRES Climate Diagnostics Center, Boulder, Colorado, USA (from their web site at http://www.cdc.noaa.gov).

NPP and export out of the euphotic zone are temporally decoupled, i.e. organic matter is often accumulated over time before it is exported (Buesseler, 1998). Much of this temporal decoupling can be removed by integrating the different production measures over a sufficiently long time. The minimum time period we will consider here as sufficient for that purpose is four months, but we readily acknowledge that this is perhaps on the low end, particularly in subtropical gyre ecosystems, where the accumulation and export of DOC is important (Carlson et al., 1994; Lomas and Bates, 2004). We therefore will consider also annual means, for which the steady-state assumption of production and export is well justified. Despite substantial averaging, these means are still subject to biases arising from under-sampling the full spectrum of variations. Episodic events, like passing eddies and/or Rossby waves with intense short-lived upwelling and nutrient supply, can contribute a significant fraction to long-term export production (McGillicuddy et al., 1998, 1999; Sakamoto et al., 2004; Lomas et al., 2005). With an average sampling frequency of a bit less than once per month, these events may have been sampled during one integration period and missed in another, potentially introducing differences between two periods that do not represent average values. This problem exists primarily for NPP and Φ_{POC}, which are based on short-term measurements, while our estimates of NCP reflect already a time-integrated estimate. Due to the long-term nature of the time-series available for the two sites (11 and 13 years, respectively), the uncertainties arising from irregularly sampled short-term episodic events are relatively small for the long-term annual and seasonal means. However, these uncertainties need to be taken into account when discussing the interannual variations of the annual means.

For this investigation we bin the data into four-month intervals by calculating means for the following periods: December through March, DJFM, April through July, AMJJ, and August through November, ASON for Sta. ALOHA, ONDJ, FMAM and JJAS for BATS. We choose different intervals for both stations to reflect the difference in the seasonal cycles, e.g. to be able to account for the stratified period at BATS that falls into JJAS. To investigate interannual variability of our data sets, we removed linear trends and a mean seasonal cycle from the original data sets (i.e. those containing one data point per variable and station occupation) by fitting a linear function and harmonic functions of 12-, 6-, and 4-month periods to the data using the method of least squares.

3. Long-term means

The long-term mean values of all quantities used in this study are listed in Table 1. NPP and POC export have approximately the same mean values at BATS and Sta. ALOHA (NPP: 13.1 ± 0.6 for BATS and $13.9 \pm 0.5\,mol\,m^{-2}\,yr^{-1}$ for ALOHA, Φ_{POC}: 0.81 ± 0.04 and 0.86 $\pm 0.04\,mol\,m^{-2}\,yr^{-1}$, respectively), while NCP at Sta. ALOHA ($3.1 \pm 0.3\,mol\,m^{-2}\,yr^{-1}$) is smaller than that diagnosed at BATS ($4.9 \pm 0.3\,mol\,m^{-2}\,yr^{-1}$). As a result, the ratio between NCP and NPP, the e-ratio, is significantly higher at BATS (0.39 ± 0.03) than at Sta. ALOHA (0.22 ± 0.03), while the mean p-ratio (the Φ_{POC} to NCP ratio) is higher for Sta. ALOHA (0.35 ± 0.03 versus 0.22 ± 0.03 at BATS). The latter ratio indicates that at Sta. ALOHA a higher percentage of the export takes place as particulate organic matter. By contrast, the fraction of NPP that is exported as particles, i.e. the pe-ratio, is 0.07 for both stations. The long-term mean for the different vertically integrated pigment concentrations are almost identical for BATS and Sta.

Table 1
Long-term mean values and standard error, i.e. one standard deviation for these means ($\sigma/\sqrt{N}$), calculated from the seasonal annual means for BATS and Sta. ALOHA

	BATS (1989–2001)				Sta. ALOHA (1989–2000)			
	All seasons	ONDJ	FMAM	JJAS	All seasons	DJFM	AMJJ	ASON
NPP	13.1 ± 0.6	11.4 ± 0.8	15.9 ± 1.0	12.3 ± 0.8	13.9 ± 0.5	11.8 ± 0.5	16.5 ± 1.0	13.3 ± 0.6
NCP	4.9 ± 0.3	2.2 ± 0.2	6.1 ± 0.5	6.5 ± 0.6	3.1 ± 0.3	1.7 ± 0.2	5.0 ± 0.5	2.6 ± 0.1
Φ_{POC}	0.81 ± 0.04	0.69 ± 0.07	0.99 ± 0.04	0.77 ± 0.06	0.86 ± 0.04	0.78 ± 0.05	0.96 ± 0.06	0.86 ± 0.06
e-ratio	0.39 ± 0.03	0.21 ± 0.02	0.40 ± 0.04	0.54 ± 0.04	0.22 ± 0.03	0.14 ± 0.02	0.33 ± 0.06	0.20 ± 0.02
p-ratio	0.22 ± 0.03	0.37 ± 0.06	0.18 ± 0.02	0.13 ± 0.02	0.35 ± 0.03	0.53 ± 0.05	0.20 ± 0.02	0.34 ± 0.02
pe-ratio	0.07 ± 0.00	0.06 ± 0.01	0.07 ± 0.01	0.07 ± 0.01	0.07 ± 0.00	0.07 ± 0.01	0.06 ± 0.01	0.07 ± 0.01
Chl-*a*	22.2 ± 1.0	20.6 ± 1.5	26.6 ± 1.7	19.5 ± 1.6	22.3 ± 0.5	21.8 ± 1.1	22.5 ± 0.6	22.6 ± 0.7
Chl-*b*	5.0 ± 0.3	5.2 ± 0.7	4.3 ± 0.4	5.5 ± 0.6	7.9 ± 0.3	7.5 ± 0.6	7.9 ± 0.6	8.5 ± 0.6
Fuco	1.1 ± 0.1	0.8 ± 0.1	1.4 ± 0.1	1.2 ± 0.4	1.0 ± 0.0	1.1 ± 0.1	1.2 ± 0.1	0.9 ± 0.1
B/A[a]	0.25 ± 0.02	0.25 ± 0.02	0.16 ± 0.01	0.29 ± 0.03	0.35 ± 0.01	0.35 ± 0.02	0.35 ± 0.02	0.37 ± 0.02
F/A[a]	0.05 ± 0.01	0.04 ± 0.00	0.05 ± 0.00	0.05 ± 0.02	0.05 ± 0.00	0.05 ± 0.00	0.05 ± 0.01	0.04 ± 0.00
T	23.4 ± 0.5	23.2 ± 0.2	20.3 ± 0.2	26.6 ± 0.2	24.8 ± 0.2	23.8 ± 0.1	24.6 ± 0.2	26.1 ± 0.1
MLD	75 ± 7	84 ± 5	116 ± 9	24 ± 2	60 ± 2	72 ± 4	51 ± 3	57 ± 2
WS	7.0 ± 0.2	7.8 ± 0.1	7.5 ± 0.1	5.6 ± 0.1	7.2 ± 0.1	6.7 ± 0.1	7.7 ± 0.2	7.1 ± 0.1

Units for the means and standard deviation are: NPP, NCP, Φ_{POC}: mol m^{-2} yr^{-1}; Chl-*a*, Chl-*b*, *Fuco*: mg m^{-2}, temperature (*T*): °C; mixed-layer depth (MLD): m; wind speed (WS): m s^{-1}; all others are without units.
[a]B/A: Chl-*b*/Chl-*a*-ratio; F/A: *Fuco*/Chl-*a*-ratio.

ALOHA; only Chl-*b* shows higher values at Sta. ALOHA (7.9 versus 5.0 mg m^{-2}). The long-term mean MLD at BATS is deeper and all physical quantities in Table 1 show stronger variations for BATS as evidenced by the higher standard deviations for temperature, MLD and wind speed.

Interpreting the mean state of the upper-ocean carbon cycle and ecosystem at both sites, we find only partial support for our conceptual model: At BATS, based on the larger seasonal variations of the MLD and the somewhat stronger intermittent forcing by small and mesoscale variability in comparison to Sta. ALOHA, one would have expected higher levels of new nutrient input and hence higher NPP. This should result in a more strongly developed export pathway and consequently a higher export ratio. While the absence of a significant difference in NPP between the two sites is inconsistent with this expectation, the higher e-ratio at BATS relative to Sta. ALOHA is consistent with this hypothesis. However, this higher export is not associated with a higher abundance of large organisms (i.e. a higher *Fuco*/Chl-*a* ratio), as expected from the presence of the export pathway. Nevertheless, the mean Chl-*b*/Chl-*a* ratio is lower at BATS than at Sta. ALOHA, indicating a smaller relative abundance of small phytoplankton, consistent with the hypothesis of a smaller importance of the regeneration loop at BATS. In summary, the higher e-ratio and the lower abundance of small phytoplankton at BATS are consistent with our hypothesis, while the absence of a significant difference of NPP and no difference in the abundance of large phytoplankton cast doubt on the predictive strength of our conceptual model.

Given the limited ability of our conceptual model to capture the observed differences between BATS and Sta. ALOHA, are the diagnostic e-ratio and the empirical pe-ratio models of Laws et al. (2000) and Dunne et al. (2005) more successful? The pelagic food web model of Laws et al. (2000) determines the e-ratio in steady state as a function of temperature and NPP. It predicts for the long-term mean e-ratio values of 0.21 for Sta. ALOHA and 0.24 for BATS. At Sta. ALOHA, the model is in good agreement with our estimate (0.22 ± 0.03), but it underestimates the long-term mean at BATS quite substantially (0.39 ± 0.03). The empirical pe-ratio model of Dunne et al. (2005) is based on a statistical analysis of data from approximately 40 oceanographic studies and describes the pe-ratio as a function of temperature, NPP and depth of the euphotic zone. It does better than the Laws et al. (2000) model and only slightly overestimates the mean pe-ratio at both stations (0.10 for BATS and 0.08 at HOT, compared to the observed value of 0.07±0.00 for both stations).

4. Long-term seasonal means

Seasonal variability at both stations is substantial. Table 1 lists the long-term seasonal means for the three four-month periods for each station (DJFM, AMJJ and ASON for Sta. ALOHA, and ONDJ, FMAM and JJAS for BATS). Fig. 2 shows the mean seasonal relationships between NPP, NCP and Φ_{POC} compared to their long-term mean relationships. The ellipses in the graphs show an estimate of the range of variations of these properties estimated from the standard deviation (σ) of the time-series of the seasonal means. These values differ from those marked by the error bars and listed in Table 1, which are the standard errors (deviations of the means, $\sigma/\sqrt{N}$), i.e. an estimate of how accurately we know the mean value. The dark shaded ellipses represent σ for the long-term mean.

The seasonal cycle at Sta. ALOHA is smaller than at BATS and exhibits more regular relationships. In particular, NPP, NCP and Φ_{POC} tend to vary linearly with each other over the seasons, i.e. their mean values in Fig. 2B, D, and F can be connected by a straight line. These lines, however, do not coincide with constant e- or p-ratios, but show a steeper trend for the e-ratio, and a lesser trend for the p-ratio. These two differing trends cancel each other, so that the seasonal relationship between Φ_{POC} and NPP very nearly follows a line of constant pe-ratio. The spring season at Sta. ALOHA (AMJJ) has the highest annual values for NPP, NCP and Φ_{POC} as well as an elevated e-ratio (0.33 compared to a long-term mean of 0.22), while winter values (DJFM) are lowest for NPP, NCP, Φ_{POC} and the e-ratio. The variability in the pigment composition over the course of the year at Sta. ALOHA is small.

These observations suggest that variability in the annual cycle at Sta. ALOHA is characterized by an intensification of the regeneration loop in spring and a weakening during fall and winter. This is in contrast to our conceptual model, which would have predicted a relatively constant regeneration loop, upon which an export pathway of seasonally varying strength is superimposed. Nevertheless, the increase in the e-ratio with increasing NPP follows our hypothesis, and the nearly linear seasonal progression is rather remarkable. However, the decrease of the p-ratio in Fig. 2D with increasing NCP is rather unexpected. Its possible reasons will be discussed below in conjunction with data from BATS.

The seasonal cycle at BATS shows similar seasonal trends to those seen at Sta. ALOHA, except for their larger seasonal amplitudes, and a tendency for a seasonal hysteresis in the relationships between NPP and NCP, and consequently Φ_{POC} (see Fig. 2A and C). Analogous to Sta. ALOHA, the winter to spring transition at BATS is accompanied by an increase in NPP and NCP, and a corresponding increase in their ratio (e-ratio). However, the spring to summer/fall transition at BATS does not follow the path of the winter to spring transition. Instead, the system deviates to an even larger e-ratio in summer/fall, primarily driven by a decrease in NPP, while NCP remains high. The seasonal evolution of Φ_{POC} in relationship to NCP (Fig. 2C) follows a hysteresis that is opposite in direction, with the summer/fall period having the lowest p-ratio. This reverse hysteresis leads to the annual progression of Φ_{POC} in relationship to NPP that follows nearly perfectly a line of constant pe-ratio (Fig. 2E). By definition, any hysteresis between NCP and NPP must be driven by changes in heterotrophic respiration. For the spring to summer/fall transition, the decrease of NPP while NCP remains nearly constant implies that NPP and heterotrophic respiration must have decreased by the same absolute amount. A possible reason for such a behavior is a seasonal change in the suitability of the synthesized organic matter to bacterial degradation. If the organic matter being synthesized becomes more refractory as the season progresses, heterotrophic respiration as a fraction of NPP will decrease, resulting in an increase of NCP as a fraction of NPP, as observed. This hypothesis is supported by the annual observation of a substantial DOC accumulation at BATS over the spring/summer time (Carlson et al., 1994; Lomas and Bates, 2004). If this explanation for the hysteresis is correct, it would imply that it would be incorrect to interpret NCP on these seasonal time-scales as a direct measure of export production, since the two measures would differ by the amount of organic matter that has accumulated in the euphotic zone over the time interval under investigation (see Hansell and Carlson, 1998, for discussion).

In contrast to Sta. ALOHA, there are distinct differences in the pigment concentrations between the seasons at BATS (see Table 1). Relative to the annual mean, the late-winter/spring (FMAM) season, when MLD are maximal (116±9 m), is characterized by lower Chl-*b* and elevated

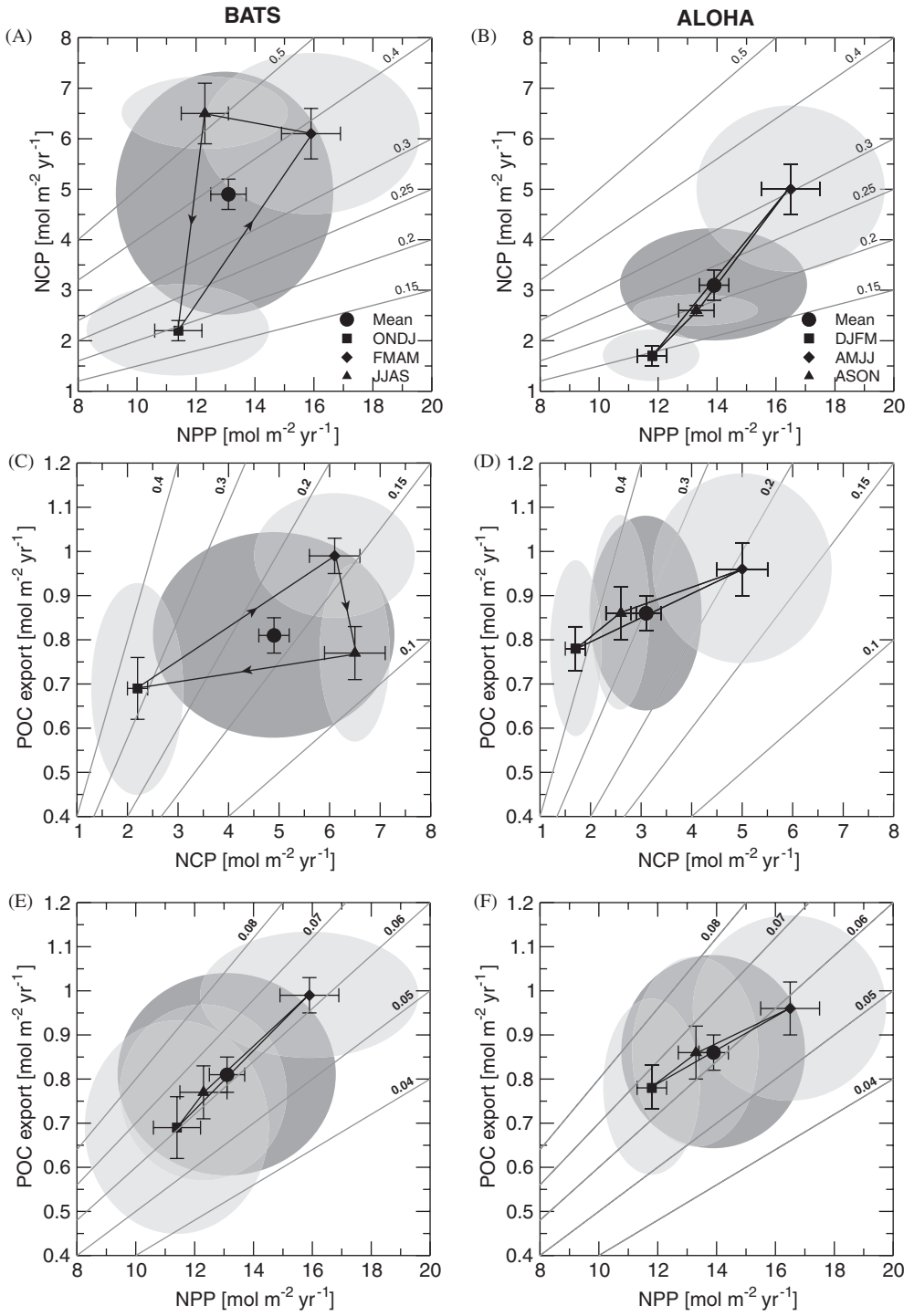


Fig. 2. Long-term mean values of NPP versus diagnosed NCP (A and B), of NCP versus Φ_{POC} (C and D), and NPP versus Φ_{POC} (E and F). Data on the left side are from BATS (Steinberg et al., 2001; Gruber et al., 2002), data on the right side are from Sta. ALOHA (Lukas and Karl, 1999; Brix et al., 2004). The lines in (A) and (B) give constant e-ratios, in (C) and (D) constant p-ratios, while in (E) and (F) the lines represent constant pe-ratios. The black circles and dark shaded ellipses represent the long-term mean values and their 1σ areas for the entire data sets, the black squares show the mean values for ONDJ (October through January) for BATS and DJFM for HOT, respectively, diamonds FMAM and AMJJ, and triangles JJAS and ASON, respectively. The axes of the ellipses represent one standard deviation (1σ) for the time-series of the seasonal means. Error bars give the standard errors (deviations of the means, $\sigma/\sqrt{N}$). The lines connecting the four seasons depict the mean seasonal evolution.

Chl-*a* and *Fuco* concentrations. Since the concentrations of *Fuco* and Chl-*a* increase similarly, their ratio remains about the same, i.e. there is no indication of a higher relative abundance of diatoms. Nevertheless, the lower Chl-*b* values indicate a decrease in small phytoplankton (and an increase in a different class of phytoplankton not covered by our pigment analysis). The situation reverses during summer/early fall (JJAS), when MLD is minimal (24 ± 2 m), resulting in the annual maximum of Chl-*b* concentrations, while *Fuco* and Chl-*a* are average or below average. This indicates that the system favors small phytoplankton during this season. The pigment data at BATS thus indicate some export pathway characteristic during spring, but otherwise this ecosystem tends to be dominated by the regeneration loop and shows many of the same characteristics as Sta. ALOHA. Although somewhat obscured by the hysteresis, the seasonal evolution of the e-ratio at BATS also follows the expected trend of increasing ratios with increasing NPP. Furthermore, the p-ratio tends to decrease with increasing NCP, leading to a nearly constant pe-ratio, whose value is nearly identical to that found at Sta. ALOHA. The finding of a decrease of the p-ratio with increasing NCP is surprising and implies that, as the export of organic matter increases at these two sites, a larger fraction of this export occurs in other forms besides sinking POC, e.g. DOC or vertically migrating zooplankton (Steinberg et al., 2000). We lack a firm explanation, but suspect that this trend in the p-ratio reflects the observation that it is the regeneration loop that responds primarily to increased nutrient supply at both sites, leading to a larger formation of DOC relative to POC. Even more surprising is that this lower than expected trend for the p-ratio at both sites leads to a near cancellation of the trend for the e-ratio, resulting in a nearly constant pe-ratio. Is this happenstance or is there a fundamental reason for this cancellation? Although we do not have an answer to this question, we can check whether this behavior is also exhibited in diagnostic and empirical models or on interannual time-scales.

The model of Laws et al. (2000) is only partially successful in capturing the seasonal variations of the e-ratio. At BATS, it fails to predict the high summer e-ratio of 0.54 derived from observations, while it does better for the rest of the year (fall/winter 0.24 versus observed 0.21, and late-winter/spring 0.30 versus 0.40). The agreement is reasonable if one considers that due to the possible seasonal decoupling of NCP and export production, our summer e-ratio estimate at BATS may be biased high. At Sta. ALOHA, the predictions of Laws' model are moderately successful in winter (0.23 versus 0.14) and spring/summer (0.21 versus 0.33), while it appears to work well for the fall (0.19 versus 0.20). The empirical pe-model of Dunne et al. (2005) is overall more successful matching the observed values, particularly in summer and fall at both stations. In winter and spring the match between model and our observation derived estimates is poor (FMAM at BATS: 0.14 versus observed 0.07, AMJJ at Sta. ALOHA: 0.10 versus 0.06). The higher success of the Dunne et al. (2005) is not surprising as it has (among other sources) been determined using data from Sta. ALOHA and BATS.

Coupled physical/biogeochemical/ecological models of different complexity and spatial dimensions have been used to investigate the seasonal cycle of biogeochemical and physical properties at Sta. ALOHA (Fennel et al., 2002; Christian, 2005) and BATS (Doney et al., 1996; Hurtt and Armstrong, 1996; Bissett et al., 1999; Oschlies et al., 2000; Hood et al., 2001; Schartau et al., 2001; Spitz et al., 2001; Anderson and Pondaven, 2003; Lima and Doney, 2004). These prognostic modeling studies focused primarily on NPP and particulate organic matter export, and did not report estimates of NCP, or of the different production ratios emphasized here, hampering a quantitative comparison of these modeling results with our hypothesis and observations. Most studies manage to simulate the observed annual cycles of NPP and Chl-*a* reasonably well. The strong variability of the MLD at BATS poses a challenge to most models using climatological forcing as the entrainment of nutrients caused by deepening winter mixed layers determines the timing and strength of the spring bloom. Most models (with the exception, perhaps, of Lima and Doney, 2004) underestimate summer NPP at BATS. The seasonal decoupling of production and particle export has been captured by Lima and Doney (2004), as well as the observed seasonal patterns of picophytoplankton and diatoms. The authors argue that lateral advection of silica and/or biomass can be an important contributor to variability at BATS. Hood et al. (2001) for BATS and Fennel et al. (2002) for Sta. ALOHA showed that nitrogen fixation is a key process that needs to be included in prognostic models in order to successfully simulate production

during otherwise nitrogen-limited periods. For Sta. ALOHA, Christian (2005) shows that the use of a flexible C:N ratio is another critical component in order to achieve a realistic representation of biogeochemical processes in the upper ocean. In general, it appears that in order for models to reproduce several constraints simultaneously, they need to use flexible elemental ratios and multiple functional groups, i.e. have the flexibility to switch between a regeneration loop and an export pathway system.

5. Interannual variability

The time-series of NPP, NCP and Φ_{POC} (displayed in Fig. 3) show substantial variability around their respective long-term mean, with a range that is in magnitude similar to the seasonal variations. The relationships between annual mean primary production and NCP for each year of the time-series is displayed in Fig. 4A and B. About half of the years gather close to their mean e-ratios (0.39 ± 0.03 for BATS, 0.22 ± 0.03 for Sta. ALOHA). At both

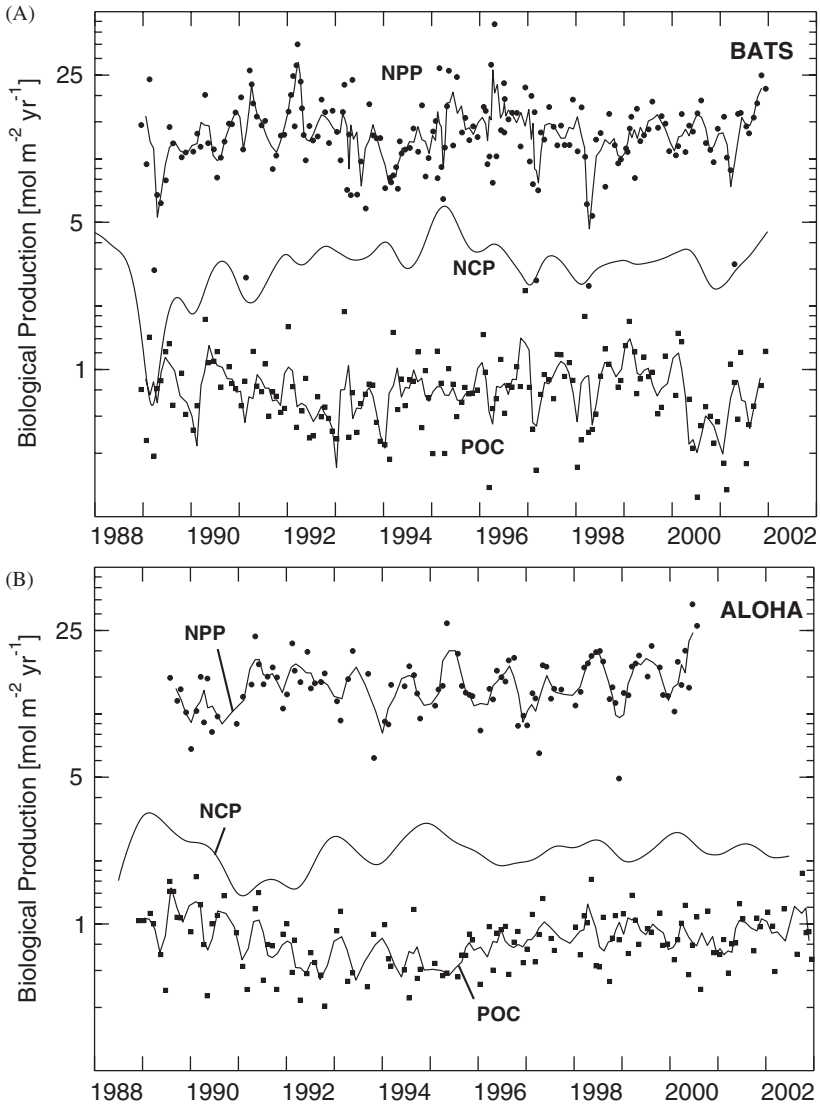


Fig. 3. Time-series of deseasonalized and detrended primary production (NPP), net community production (NCP) and particulate carbon export (Φ_{POC}) in mol m^{-2} yr^{-1} for BATS (A) and Sta. ALOHA (B). The ordinate has a logarithmic scale. Solid circles represent measurements, while the lines for NPP and POC are running averages to emphasize interannual variability (three-point average). The NCP lines represent a smoothing spline.

stations, we observe notable deviations from the long-term mean e-ratios with values between 0.25 and 0.54 at BATS and between 0.18 and 0.43 for Sta. ALOHA. The p-ratios for both stations are depicted in Fig. 4C and D and show similarly large variations around their long-term means. In contrast to the seasonal evolution, the large variations in the e- and the p-ratio do not cancel each other on interannual time-scales, so that the pe-ratios (Fig. 4E and F) also exhibit very large interannual variability for both stations with a range from 0.04 to 0.09 around the long-term mean of 0.06 ± 0.02. At Sta. ALOHA about half of the years in our study track the mean almost exactly, most other years have notable deviations (see also Karl et al., 2003a). Our new analysis does not confirm our previous suggestion of a tendency for years with low pe-ratios to have lower e-ratios at Sta. ALOHA (Brix et al., 2004). This previous result is likely erroneous, induced by their using a fixed scaling factor to extrapolate the mixed layer estimates of NCP to the entire euphotic zone, while the variable scaling factor employed here is clearly better justifiable.

What are the factors driving these substantial interannual variations in the relationships between NPP, NCP, and Φ_{POC}? We have partial answers. For example, Lomas and Bates (2004) pointed out for BATS that from 1992 to 1995, the winter/spring accumulation of DOC, a precondition for export of DOC, was high and, with the exception of 1995, associated with lower POC fluxes. This is consistent with the low p-ratios we find for 1992 through 1995 as (1 minus p-ratio) is the fraction of export going into DOC or other means of export.

To explore the possible driving factors more thoroughly, we calculated correlations between all our quantities using time-series of the annual means. The *r*-values are given in Tables 2 and 3 with significant values (at a 95% confidence level) in *larger print*. Given the degree to which the data points in all graphs of Fig. 4 are scattered, it is not surprising that we do not find significant correlations between NPP, NCP and Φ_{POC}.

Variables associated with meteorological forcing show only few significant correlations with production and export quantities. At BATS, we find a positive correlation ($r = +0.61$) between temperature and the e-ratio, an anti-correlation between MLD and the pe-ratio ($r = -0.70$) and a positive correlation of wind speed with NPP ($r = +0.75$). For Sta. ALOHA, none of the meteorological quantities that we investigated yielded significant results. We also used winter means instead of annual means for temperature, MLD and wind speed, based on the idea that much of the variability throughout the year, particularly at BATS, is determined by the processes in winter, when MLD is maximal, stratification weakest, and hence nutrient supply at its peak. Although we find correlations values to be generally higher for winter means, the results do not provide any additional significant relationships between our quantities. Correlations with indices of large-scale phenomena like ENSO, the North Atlantic and the Pacific Decadal Oscillation are small and consequently not statistically significant (not shown).

The few significant correlations that we have been able to identify are generally not supportive of our hypothesis. For example, we would have expected a negative correlation between temperature and the e-ratio, as higher temperatures usually accelerate heterotrophic respiration, leading to a decrease of NCP relative to NPP. Similarly, the negative correlation between MLD and the pe-ratio is also inconsistent with our expectation, since we would have expected that deeper MLD would imply a larger input of new nutrients into the euphotic zone, fueling the export pathway, and leading to a larger fraction of NPP being exported in the form of POC.

We find that interannual variations in meteorological forcing have little statistical power to explain the large interannual variations in the relationships between NPP, NCP and Φ_{POC}, and where they do, they do not support our hypothesis. Since most considered meteorological parameters are only indicators of the controlling processes, e.g., we used MLD as an indicator for convective nutrient supply, we need to take a closer look at the biological indicators, i.e. pigments.

Chl-*a* and *Fuco* are significantly positively correlated with NCP at both stations (Chl-*a*: $r = +0.71$ and $r = +0.66$, *Fuco*: $r = +0.71$ and $r = +0.74$ for BATS and Sta. ALOHA, respectively). At BATS Chl-*a* is also correlated with NPP ($r = +0.64$), but not at Sta. ALOHA ($r = - - 0.18$); In contrast, Chl-*a* and *Fuco* are significantly correlated with the e-ratio at Sta. ALOHA ($r = +0.61$ and $r = +0.64$), but not at BATS ($r = +0.03$, and $r = +0.21$). All pigments have significant positive correlations with each other at both stations, implying that the phytoplankton groups tend to vary in concert with each other. Given the positive correlation of Chl-*a* and NCP, these inter-pigment correlations

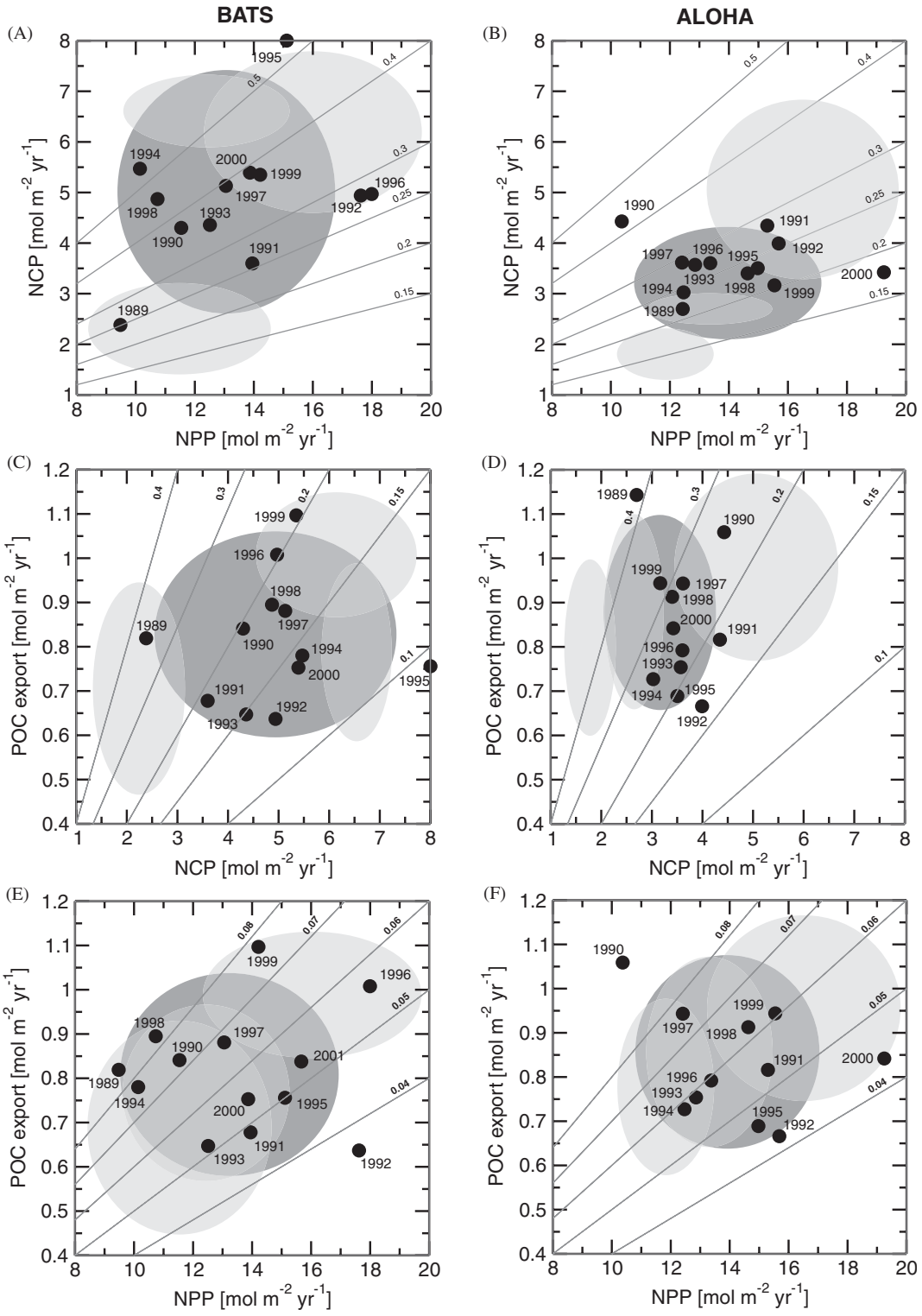


Fig. 4. As in Fig. 2 but for annual mean values for the individual years. The gray ellipses showing the long-term annual mean and seasonal means are repeated from Fig. 2 to provide a reference.

Table 2
Correlations between the time-series of interannual anomalies of various observed quantities at BATS from 1989 to 2001. Correlations with $p<0.05$ are *slanted and in larger print*. The correlations were computed for annual means

	e-ratio	p-ratio	pe-ratio	NPP	NCP	Φ_{POC}	B/A[a]	F/A[a]	Chl-*a*	Chl-*b*	*Fuco*	T[b]	MLD[b]	WS[b]
e-ratio	1.00	−0.47	0.34	−0.42	*0.65*	0.10	−0.03	0.27	0.03	0.00	0.21	*0.61*	−0.58	−0.14
p-ratio		1.00	*0.65*	−0.44	*−0.79*	0.37	−0.29	−0.04	−0.33	−0.34	−0.26	−0.41	−0.16	−0.46
pe-ratio			1.00	*−0.78*	−0.27	0.57	−0.26	−0.39	−0.38	−0.34	−0.53	0.14	*−0.70*	−0.53
NPP				1.00	0.39	0.04	0.33	−0.02	*0.64*	0.54	0.39	−0.19	0.56	*0.75*
NCP					1.00	0.19	0.23	0.37	*0.71*	0.50	*0.71*	0.41	−0.13	0.48
Φ_{POC}						1.00	−0.09	−0.11	0.24	0.07	0.05	0.13	−0.51	0.12
B/A[a]							1.00	0.41	0.46	*0.90*	0.56	0.14	0.40	−0.06
F/A[a]								1.00	0.20	0.36	*0.79*	0.26	0.18	0.09
Chl-*a*									1.00	*0.80*	*0.75*	−0.19	0.17	0.54
Chl-*b*										1.00	*0.74*	0.00	0.34	0.22
Fuco											1.00	0.05	0.25	0.40
T[b]												1.00	−0.58	−0.31
MLD[b]													1.00	0.48
WS[b]														1.00

Units for the means and standard deviation are: NPP, NCP, Φ_{POC}: mol m^{-2} yr^{-1}; Chl-*a*, Chl-*b*, *Fuco*: mg m^{-2}, T[b]: °C; MLD[b]: m; wind speed: m s^{-1}; all others are without units.
[a]B/A: Chl-*b*/Chl-*a*-ratio; F/A: *Fuco*/Chl-*a*-ratio.
[b]T: temperature, MLD: mixed-layer depth, WS: wind speed.

Table 3
As in Table 2, except for Sta. ALOHA

	e-ratio	p-ratio	pe-ratio	NPP	NCP	Φ_{POC}	B/A[a]	F/A[a]	Chl-*a*	Chl-*b*	*Fuco*	T[b]	MLD[b]	WS[b]
e-ratio	1.00	−0.29	0.54	*−0.65*	*0.75*	0.24	0.19	0.39	*0.61*	0.57	*0.64*	−0.16	−0.25	0.13
p-ratio		1.00	*0.64*	−0.31	*−0.70*	*0.82*	0.40	0.20	0.25	0.44	0.29	−0.06	0.40	0.10
pe-ratio			1.00	*−0.81*	−0.03	*0.90*	0.32	−0.13	−0.25	0.02	−0.23	−0.20	0.18	0.21
NPP				1.00	−0.01	−0.50	−0.20	0.04	−0.18	−0.26	−0.10	0.03	0.03	−0.29
NCP					1.00	−0.18	0.10	0.53	*0.66*	0.54	*0.74*	−0.08	−0.41	−0.16
Φ_{POC}						1.00	0.39	0.20	0.20	0.38	0.26	−0.26	0.35	0.11
B/A[a]							1.00	0.57	0.05	*0.74*	0.41	0.27	−0.47	−0.33
F/A[a]								1.00	0.28	*0.61*	*0.81*	−0.30	−0.25	−0.30
Chl-*a*									1.00	*0.70*	*0.78*	−0.40	0.17	0.19
Chl-*b*										1.00	*0.83*	−0.07	−0.25	−0.11
Fuco											1.00	−0.43	−0.06	−0.07
T[b]												1.00	*−0.64*	*−0.65*
MLD[b]													1.00	0.49
WS[b]														1.00

[a]B/A: Chl-*b*/Chl-*a*-ratio; F/A: *Fuco*/Chl-*a*-ratio.
[b]T: temperature, MLD: mixed-layer depth, WS: wind speed.

indicate that elevated total export (NCP) tends to be driven by an increase of all considered phytoplankton classes. This general behavior differs from that described by Lomas and Bates (2004), who found for years with elevated DOC accumulation and export at BATS increased relative abundance of Haptophytes compared to Prochlorophytes, i.e. a shift in community structure from smaller to larger phytoplankton communities. This discrepancy continues to exist upon closer inspection of the correlations in Table 2, since it shows relatively large negative, albeit not significant, correlations between both Chl-*b* and the Chl-*b*/Chl-*a* ratio and the p-ratio, suggesting that years with a higher ratio of export going to DOC (low p-ratio) tend to coincide with years of higher relative abundance of small phytoplankton. Possible reasons for this discrepancy could be that Lomas and Bates (2004)

investigated winter/spring bloom maxima (while we are focusing here at annual means), and their use of a bigger suite of pigments. Our choice of three pigment groups might be too restrictive for a substantiated comparison with their study. Steinberg et al. (2001) reported interannual variability of nutrient fluxes, primary production, and chlorophyll biomass at BATS to be largely tied to variability of wintertime mixing with deep mixing associated to high biological production. Our investigations show some of these characteristics, e.g. MLD and NPP, are positively correlated ($r = +0.56$), but none of them pass the 95% confidence level. In fact, there is a remarkable absence of statistical power in any of the investigated parameters.

A similar lack of statistical predictability is found in the diagnostic and empirical models of the e- and pe-ratio of Laws et al. (2000) and Dunne et al. (2005). As shown in Figs. 5 and 6, respectively, the interannual maxima and minima, as well as the amplitude of variability, differ substantially between the Laws and Dunne models and our observations.

Overall, the results of our correlation analysis as well as the results of the comparison between the diagnostic and empirical models and the observations reveal that none of the investigated parameters is able to capture the observed large interannual variations. An analogous analysis performed with a time-series of seasonal means did not provide differing results. We therefore find no evidence of support for our hypothesis in the analyses of interannual variations in the relationships between NPP, NCP and Φ_{POC}.

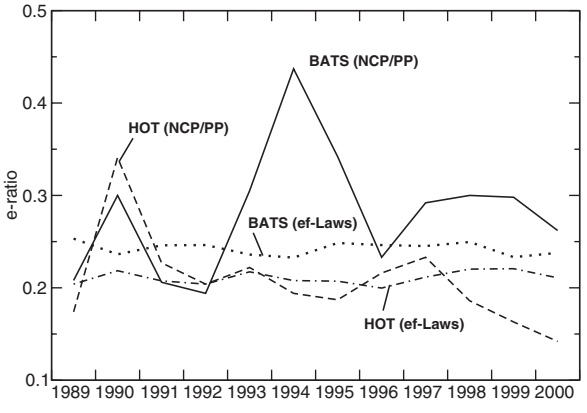


Fig. 5. Time-series of annual mean values of e-ratios (NCP/NPP) for BATS (solid line) and Sta. ALOHA (dashed). The dotted and dashed-dotted lines represent the expected values based on the model of Laws et al. (2000) using annual means of temperature and NPP as input.

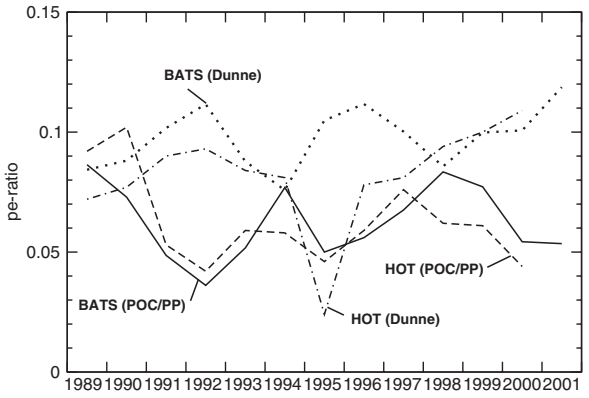


Fig. 6. Time-series of annual mean values of pe-ratios (Φ_{POC}/NPP) for BATS (solid line) and Sta. ALOHA (dashed). The dotted and dashed-dotted lines represent the expected values based on the empirical model of Dunne et al. (2005) using annual means of temperature and NPP as input.

6. Discussion

Our findings suggest that the concept of a regeneration loop and an export pathway is applicable to a comparison of the two JGOFS sites Sta. ALOHA and BATS to a limited extent only. Even in the long-term mean, we find evidence only for parts of our hypothesis. Seasonal variations at Sta. ALOHA appear to be a result of an intensification or weakening of the regeneration loop while at BATS the export pathway is temporally "activated" in spring. Interannually, we find almost no significant correlations between physical forcing, ecosystem composition, and the various production and export measures. Also, the diagnostic and empirical models do a poor job simulating variability at both time-series sites. Why is this so?

Before we can discuss this question, we need to eliminate the possibility that the employed data are not robust enough for this type of analysis. In the cases of the seasonal and long-term means, the large number of samples (>100) lead to very precise estimates of mean NPP, NCP, and Φ_{POC}, even in the presence of episodic events like pulses of nutrient import triggered by passing eddies, Rossby waves and/or atmospheric deposition events. This is because the time-series are sufficiently long to ensure that they have sampled a large enough fraction of the probability density function to

determine the mean and the first moment with reasonable confidence. This is less the case for the interannual time-series of the annual means, as the latter usually include only 10–12 samples, introducing the possibility that under-sampling of the variations leads to biases. We suspect that at least part of the high scatter in the interannual analyses is driven by such under-sampling.

A more serious problem are methodological uncertainties in the various estimates as they can lead to biases that are difficult to predict. NPP, NCP and Φ_{POC} are all subject to non-negligible uncertainties, such as, for example, in the case of NPP arising from uncertainties in the required length of incubation, the role of autotrophic respiration, etc. (see discussion above and Marra, 2002). In the case of NCP, we need to be concerned with the extrapolation of mixed-layer estimates to the whole euphotic zone and uncertainties arising from the many inputs that go into the budget equations (see Gruber et al., 1998, for a discussion of errors and uncertainties in NCP). Finally, sediment-trap-based estimates of Φ_{POC} are notorious for biases, associated with the removal of "swimmers" and a number of hydrodynamic issues (see Buesseler et al., 2006, for a recent assessment). The magnitude of these biases is not well known, but we estimate that the biases for NPP and NCP are unlikely larger than 30%, which is generally smaller than the observed signals. Biases in Φ_{POC} were shown to be larger, ranging from an underestimation by nearly a factor of 2 for Sta. ALOHA (Benitez-Nelson et al., 2001) to a 30% under-estimation for BATS (Buesseler et al., 2000), with an indication of a seasonal change in the trapping efficiency. We therefore have substantially less confidence in Φ_{POC} than we have in NPP and NCP. Another limitation is our restriction to three pigment groups and hence our disregard of the possible influence of other phytoplankton communities, which might limit our ability to interpret community structure shifts. While the latter limitation could be overcome with more sophisticated pigment analysis tools such as ChemTax (Mackey et al., 1996), we doubt that this would result in substantial changes in our interpretation of the pigment data. In summary, while we cannot exclude the possibility categorically that biases in the data mask existing trends or create patterns that do no exist, we consider their effect not to be large enough to explain our observations.

If we accept that the methodological and sampling limitations can be excluded as a cause, we see three possibilities why the conceptual approach used in this study is falling short: first, our conceptual model is wrong. Although our analyses have provided little direct evidence in support of this conceptual model, its success in explaining zeroth order, global-scale variations in ecosystem structure and relationships between NPP, NCP and Φ_{POC} (e.g. Laws et al., 2000) suggest it to be valid at least at these scales. Second, the upper ocean ecosystem in the subtropical gyres is not deterministic, i.e. there exists no fixed and predictable response of the system to a certain forcing. Ecological systems have indeed multiple equilibria and often show complex transient behavior around attractors (e.g. Sabin and Summers, 1993; Scheffer et al., 2001), lending support to this explanation. Third, the physical and biogeochemical characteristics of the two time-series sites are too similar to each other and the range of seasonal to interannual variations too small to really cause substantial structural differences. Both sites are located in oligotrophic regions, and with the exception of a stronger seasonality at BATS, have rather similar forcing. The export pathway may exist at BATS too intermittently to cause a statistically significant difference from Sta. ALOHA in our seasonal to annual analyses. With regard to the limitations of the diagnostic and empirical models, Dunne et al. (2005) already pointed out that their algorithm appears to capture global relations but shows an "unfortunate lack of applicability" to within-site variance.

In summary, it appears the lack of support for our working hypothesis stems from a combination of causes. While we argued that the limitation in the data are not the leading cause, these limitation are nevertheless substantial and present a formidable challenge to our ability to quantitatively understand ocean productivity and the fate of the fixed carbon. Putting the data limitation issue to the side, we suspect that it is the limited magnitude of the within-site and between-site variance in the physical forcing that prevents the two ecosystems from escaping their regeneration loop dominance to a significant degree. Given the absence of strong variations in external forcing, the observed variability in the system is then perhaps primarily driven by ecosystem internal processes with their inherent lack of predictability, preventing our simplified conceptual models from having predictive power.

7. Summary and conclusions

We examined the relationship between NPP, NCP and Φ_{POC} and their connection to ecosystem structure and physical forcing using data from the JGOFS stations ALOHA and BATS. Our aim was to elucidate the environmental controls that favor the export pathway typically dominated by larger phytoplankton over the regeneration loop typically dominated by smaller phytoplankton. Our hypothesis was that higher nutrient input elevates primary production, and that this favors larger phytoplankton, which then cause an intensification of the export pathway.

This hypothesis holds for long-term means when comparing the two sites, although we could not confirm that higher than normal export is connected to larger phytoplankton. Biological production and export at BATS are dominated by the influence of winter MLD variations and show partial "export pathway characteristics," while at Sta. ALOHA the regeneration loop is dominant. Seasonal long-term means follow this pattern only partially. "Export pathway characteristics" at BATS exists only in spring, while the system appears to return to a regeneration loop state in summer and fall. On interannual time-scales, we fall short of showing statistically significant patterns that would allow us to characterize the system as being in one state or another.

The diagnostic and empirical models of Laws et al. (2000) and Dunne et al. (2005) are reasonably successful in predicting the long-term mean, but fail to predict seasonal and interannual variability of the e- or pe-ratio at our sites. We attribute the deficiencies of these models as well as part of the lack of success of our hypothesis to a possible lack of predictability resulting from the system not being deterministic. In addition, the characteristics of the two time-series sites may not be distinct enough and the range of variations on seasonal and interannual time-scales may not be large enough to establish statistically significant variations in ecosystem structure and relationships between NPP, NCP and Φ_{POC}. Finally, possible biases in the various production measures as well as the limited length of the time-series (in the case of the interannual analyses) unfortunately cannot be ignored.

It will be interesting to revisit the questions and uncertainties laid out here when longer time-series are available. These will include a higher number of episodic events and allow a more detailed interpretation, particularly on interannual time-scales. Of particular interest would be the ability to catch aperiodic bursts of production, which could activate the export pathway for very brief periods, and which have not been well captured by the time-series so far. This requires autonomous instrumentation, such as placed on moorings (cf Letelier et al., 2000; Sakamoto et al., 2004 for Sta. ALOHA), gliders, or other platforms. Efforts to this end are currently underway, and it will be of great interest to use such high-resolution data to test our conceptual model on short time-scales. An additional improvement consists in a more careful and extensive consideration of the pigment data, permitting to investigate changes in phytoplankton community structure in greater detail. Finally, an important extension of the investigations performed here would be to include data from different biomes spanning a substantially wider range of biogeochemical provinces and behavior.

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