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Primary production, new production and vertical flux in the eastern Pacific Ocean

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The sinking of particulate organic matter in the ocean links food webs beneath the euphotic zone to surface primary production and is an important pathway for the downward transport of many elements[1–3]. The flux of particulate organic carbon (POC) is also an important parameter in the global carbon cycle and may be related to long-term changes in atmospheric CO_2[4,5]. In 1980, Suess[6] synthesized existing measurements from sediment trap studies into a model to predict the vertical flux of POC from depth (z) and primary production (PP)[6]. The Suess model has become the standard for evaluating vertical flux data[7], for estimating the annual flux of POC in the ocean[8] and for parameterizing ocean carbon cycle models[4,5]. We present here a new model of the vertical flux of POC and particulate organic nitrogen (PON) from a set of contemporaneous measurements of PP and fluxes made during the VERTEX (Vertical Transport and Exchange) programme in the north-east Pacific. The VERTEX model indicates that PP and vertical fluxes of POC and PON, in the oligotrophic ocean are greater than previously suggested. In addition, the vertical flux of PON from the photic zone represents a measure of the PP that is supported by new nitrogen (new production)[9,10]. In the north-east Pacific, new production ranged from 13 to 25% of primary production and was positively related to total PP.

The vertical flux of POC and PON in the upper 2,000 m of the water column was measured using free floating particle traps[11] at nine sites in the Pacific Ocean[12,13]. While traps were deployed, PP was measured at each site, using the heavy-metal-free ^{14}C method (ref. 14). Trapped materials were preserved, in a formalin solution[15], as collected to avoid losses due to decomposition. Some organics undoubtedly partition from the particulate to dissolved fraction during preservation so the particulate fluxes measured in sediment traps represent conservative estimates[15,16]. All collections were also examined microscopically and zooplankton which had entered the traps alive during the deployment were removed before measurement of POC and PON[15].

The VERTEX data were $\log_{10}$-transformed and relationships for POC and PON were derived using multiple regression with z and PP as independent variables. We chose to express the data in terms of mg m^{-2} d^{-1} instead of the units of g m^{-2} yr^{-1} used in previous models to reflect more accurately the timescale of the measurements. The following equations for POC and PON were obtained:

$$\mathrm{POC} = 3.523\, z^{-0.734}\mathrm{PP}^{1.000} \quad (1)$$

$$\mathrm{PON} = 0.432\, z^{-0.843}\mathrm{PP}^{1.123} \quad (2)$$

where z is restricted to depths between the bottom of the euphotic zone and 2,000 m.

For comparison, we recalculated in terms of daily flux the original data from the model of Suess[6] and a reformulation of a limited portion of the same data by Betzer *et al.*[7] (Table 1). All models are highly significant; however, the amount of variance explained (r^2) in the VERTEX models is lower than previous models (Table 1). We attribute this partly to the higher variability that might be expected in contemporaneous measures of PP and flux relative to the averages of historical data used in previous models. In addition, increased flux rates with depth were occasionally observed, implying that horizontal advection of particles and *in situ* particle production may occur at specific depths[12,17,18].

The partial regression coefficients indicate the form of the relationship between vertical flux and the independent variables. For all three POC regressions, the partial regression coefficients for z are significantly <-1 (t-test, all $P<0.001$). The nonlinear change in the relationship between flux and depth indicates, not unexpectedly[19], that most particulates are transformed to biomass, dissolved organics, and inorganic end products in the

Table 1 Summary of multiple regression models to predict the vertical flux of particulate organic carbon (POC) and nitrogen (PON) in mg C or N m^{-2} d^{-1} from depth (z) in metres and primary production (PP) in mg C m^{-2} d^{-1}

Source	n	B_0	B_1	±95% CI	Range	$\bar{Z}$	B_2	±95% CI	Range	$\overline{PP}$	r^2	F	CF
Suess POC	33	−0.503	−0.567	0.104	50–5,582	780	1.302	0.164	110–1,644	345	0.97	507	1.066
Betzer *et al.* POC	27	−0.574	−0.627	0.121	100–5,582	1,392	1.415	0.151	110–1,644	272	0.97	433	1.043
VERTEX POC	74	0.547	−0.734	0.143	50–2,000	497	1.000	0.357	245–1,140	517	0.69	79.3	1.221
VERTEX PON	74	−0.364	−0.843	0.139	50–2,000	497	1.123	0.345	245–1,140	517	0.76	114	1.205

Data were $\log_{10}$ transformed and fitted to the equation $\log_{10}\mathrm{Flux} = B_0 + B_1 \log_{10} z + B_2 \log_{10}\mathrm{PP}$. Additional statistics are the means and ranges of the data used in each model as well as the coefficient of determination (r^2) and F-value from the multiple regression analysis of variance (for all 4 models $P<0.0001$). Predictions in arithmetic units from these logarithmic regressions must be corrected for bias introduced in back transformation using the calculated correction factor (CF)[27].

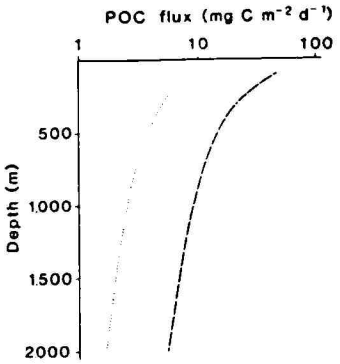


Fig. 1 Comparison of the Suess (dotted line) and VERTEX (dashed line) models at primary productivities representative of oligotrophic oceanic conditions. For the Suess model a historical average PP of 100 mg C m^{-2} d^{-1} was used. For the VERTEX model the median measured oceanic PP of 400 mg C m^{-2} d^{-1} was used.

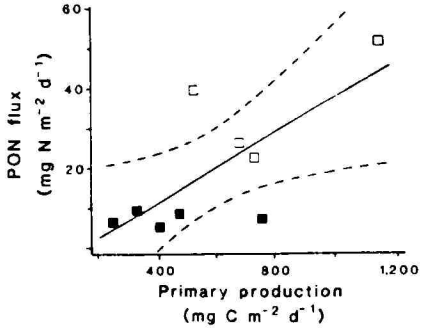


Fig. 2 Relationship between primary production and vertical flux of particulate organic nitrogen (PON) measured in traps located at the base of the euphotic zone for nine VERTEX stations. Regression model: PON = 0.0439 PP − 6.17, $r^2 = 0.52$, $F = 7.57$, $P < 0.01$. Solid squares represent stations with deep euphotic zones (≥100 m) and open squares represent stations with euphotic zones of 50 m. Broken lines are the 95% confidence intervals for the regression.

upper water column. The partial regression coefficients for PP are typically >1, but not significantly so for the VERTEX models. The hypothesis that the ratio of flux to production increases with PP ($B_2 > 1$) (see ref. 7) is not supported by the VERTEX data.

The PP data used in the Suess model reflect historical measurements and are lower than measurements made in the VERTEX programme. For example, daily productivities of the order of 100–150 mg C m^{-2} d^{-1} were considered representative of oligotrophic oceanic conditions[6]. Measurements of PP made at 5 oligotrophic sites during VERTEX ranged from 245–760 mg C m^{-2} d^{-1} with a median value of 400 mg C m^{-2} d^{-1}. Figure 1 compares predicted POC fluxes for the Suess and VERTEX models at PP of 100 and 400 mg C m^{-2} d^{-1} respectively. The VERTEX model POC fluxes are 3–5 times greater (depending on depth) under these conditions. The actual rates of PP in the open ocean have recently been intensely debated[20–25]. The VERTEX data, although limited, support the notion that oceanic PP is higher than historical estimates and that the vertical flux of sinking particles is also greater.

The flux of PON from the euphotic zone represents a measure of new production, since this flux must ultimately be balanced by inputs of nitrogen to the euphotic zone[9,10]. For the nine study sites, the relationship between PP and the flux of PON is significant (Fig. 2). Using the linear regression model of Fig. 2 and assuming a C/N ratio of 6.6, new production as a percentage of the total increases from 13 to 25% over the PP range of 245–1,140 mg C m^{-2} d^{-1}. Confidence, however, in any prediction of new production from measures of PP and our model is poor (Fig. 2). This might be interpreted as support for the notion of high variability in new production[24], but for most oligotrophic sites studied with euphotic zone depths ≥100 m ($n = 5$, solid squares, Fig 2), new production as measured by PON flux was relatively constant: $\bar{x} \pm 1$ s.d. = 7.23 ± 1.59 mg N m^{-2} d^{-1} (Fig. 2). If we convert the daily mean new production value for oligotrophic conditions to an annual rate by multiplying by 365 and assuming a Redfield C/N ratio of 6.6, the estimate of 17.4 ± 3.83 g C m^{-2} yr^{-1} is reasonably close to the value of 25.2 ± 6.96 g C m^{-2} yr^{-1} recently estimated for the Sargasso Sea[23]. Our value, however, is significantly less than the 50 g C m^{-2} yr^{-1} estimated by Jenkins and Goldman[23]. The data are clearly too limited to provide an accurate estimate of new production, given the potential spatial and temporal variability. A VERTEX seasonal study to measure the variability in PP and PON flux over an annual cycle at an oceanic site is now underway.

The empirical models of vertical flux allow prediction of the rate of loss of organic matter from the photic zone, the transformation of this material in the mesopelagic zone, and input to the deep sea. We conclude that the magnitude of vertical flux in the ocean may be greater than previous models based on PP suggest, because oceanic PP may be higher than historical averages. The coupling of models of vertical flux as developed in the VERTEX study with improved models of circulation and PP based on remote sensing will substantially enhance our knowledge of the flux and cycling of materials on seasonal, regional and basin-wide scales in the ocean[26].

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