Determining primary production from the mesoscale oxygen field

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Net biological oxygen production can be determined from models of time-series measurements of the oxygen field, so long as there are simultaneous measurements of inert gas tracers to estimate the role of air-water transfer and mixing with the ocean interior. In the two locations where this has been done, the oxygen balance yields net nutrient production values that are within a factor of three of sediment trap and in vitro incubation experiments. Initial findings from a similar study at the US JGOFS time-series station near Hawaii (Station ALOHA) reveal that nitrogen uptake determined by net biological O₂ production in the upper 175 m, which includes both the euphotic and shallow respiration zones, agrees to within a factor of two of the mean annual sediment trap N flux at 150 m. Poorly known processes that should be explored to reconcile differences in the various methods are: (a) transport of dissolved and suspended particulate organic matter out of the euphotic zone, (b) alteration of O₂:DIC:NO₃ stoichiometry in the euphotic zone by production of carbon-rich dissolved organic matter, and (c) bacterial heterotrophic NO₃ uptake.

Introduction

The influence of biological processes on oxygen concentration in the upper ocean is well known, but the oxygen distribution has only recently been exploited to derive quantitative estimates of biological production. Schulenberger and Reid (1981) calculated net oxygen production from historical measurements of the shallow oxygen maximum in the central North Pacific. Jenkins and colleagues (Jenkins and Goldman, 1985; Musgrave et al., 1988; Spitzer and Jenkins, 1989) demonstrated the power of the approach with the study of oxygen production in the euphotic zone using data from the time series at Station S near Bermuda. A similar approach has been applied at the other prominent location of time-series data, Station Papa, in the subarctic Pacific (Emerson, 1987; Emerson et al., 1991; Thomas et al., 1990; Quay et al., 1992; Archer et al., 1992). Estimates of net biological oxygen production reported by Schulenberger and Reid (1981) and Jenkins and Goldman (1985) were much greater than expected from traditional productivity measurements determined by daily ¹⁴C incubations and the relationship between net production and export flux (the f-ratio described by Eppley and Peterson, 1979). The results from the subarctic Pacific, however, generally agree with the biological measurements and traditional concepts (Emerson, 1987; Emerson et al., 1991). Since in vitro ¹⁴C incubations are deployed for a period of one day or less, and oxygen mass balance determinations average over weeks, the two are not comparable if productivity is intermittent, which is likely the case in the oligotrophic, subtropical ocean (but less likely in high latitudes where phosphate and nitrate do not limit production). Periods of high productivity in the subtropical gyres are probably under-represented by infrequent daily incubations (Jenkins and Goldman, 1985). This can lead to low new production estimates calculated from improper averaging of ¹⁴C net production and f-ratio measurements (Platt and Harrison, 1985; Platt et al., 1989).
Mass balance determinations of net biological oxygen production have played an important role in oceanography by providing an alternative estimate of net community production (or export production) and by stimulating interest in the accuracy of various methods used to determine biologically mediated fluxes from the upper ocean. One cannot be confident of our ability to determine export fluxes until a number of approaches yield the same result or until differences among the results are mechanistically understood. We present a very brief description of the mechanisms controlling oxygen mass balance in the upper ocean, then compare the relationships among net oxygen production and independent measures of net nutrient flux where the data are available, and, finally, describe initial results of an oxygen mass balance at the US JGOFS Hawaii Ocean Time Series Station.

Processes controlling the oxygen balance in the upper ocean

The common feature of oxygen mass balance studies is a time course of data. Since the upper ocean is rarely at steady state with respect to biological or physical forcing, even on weekly time scales, knowledge of the temporal change of concentration is essential for quantitative interpretation. Fluxes that must be estimated to derive a measure of the biological oxygen production (Fig. 1) are air-water gas exchange, air injection by bubbles formed from breaking waves, and transport between the upper ocean and deeper water.

Gas transfer between ocean surface waters and the atmosphere is usually separated into a concentration gradient-driven gas flux and an air injection flux. The first is parameterized as the product of a mass transfer velocity, \( G (\text{m d}^{-1}) \), and the difference between the gas concentration at equilibrium with the atmospheric partial pressure, \([C_a]\) (mol m\(^{-3}\)), and that measured in the mixed layer, \([C_m]\):

\[
F_G = -G([C_m] - [C_a])
\]  

Relationships among transfer coefficients for different gases at low to moderate wind speeds are dependent on the molecular diffusion coefficient \(D\) to the power 1/2 (Jähne et al., 1984; Ledwell, 1984).

\[
G_c = \frac{(D_c/D_{O_2})^{1/2}}{} \frac{G_{O_2}}{}
\]  

Attempts to generalize the relationship between tracer-determined mass transfer coefficients and forcing processes have met with limited success. Empirical correlations to wind speed are useful but, by themselves, lack highly accurate prediction capability because other mechanisms are important in controlling the gas exchange rate, and because of a time and space scale mismatch between tracer-determined transfer coefficients and wind speed measurements. Wanninkhof (1992) recently reviewed these problems and derived a wind-speed gas transfer velocity relationship that is greater than the one widely adopted by Liss and Merlivat (1986), particularly at high wind speeds. Data exist to support both formulations.

During wave breaking, air bubbles are injected below the air–water interface, where pressures are greater than at the surface. The bubbles partially or totally collapse and exchange their contents with the surrounding waters. This mechanism would create a standing super-

![Figure 1. Schematic depiction of the oxygen mass balance in the upper ocean. P is photosynthesis and R respiration. The equation is generalized: nutrients are deleted and organic matter is represented as CH\(_2\)O.](https://example.com/image)
saturation of atmospheric gases of 0.5 to 2% in the absence of any other process (Woolf and Thorpe, 1991), because a gas exchange flux to the atmosphere is created to balance the air injection. Since observed oxygen supersaturations are in the range of a few percent, air injection must be evaluated to calculate the function of supersaturation that is biologically produced.

Jenkins (1988) and Spitzer and Jenkins (1989) determined a relationship between the air injection flux, \( F_b \), and wind speed at Station S using the tracers \(^{3}\)He and argon:

\[
F_b = a_i a_{inj} (f_i + f_p) 6 \times 10^{-8} (U_{10}/10)^y
\]

(3)

Here \( a_i \) is the gas mole fraction in the atmosphere; \( a_{inj} \) is an empirical parameter adjusted to fit the data at Bermuda; \( f_i \) and \( f_p \) are the relative fractions of total and partial bubble collapse (Jenkins, 1988), \( f_i + f_p = 1; \) \( \Gamma \) is the 2/3 power of the ratio of the diffusion coefficient of the gas of interest to that for He at 20°C; \( U_{10} \) is the wind speed (m s\(^{-1}\)) at 10 m height; and \( y \) is the wind speed exponent. Empirical values derived from the best fit to the annual argon measurements at Bermuda are \( a_{inj} = 0.39, f_i = 0.07, \) and \( y = 2.2 \). Wallace and Wirick (1992) recently compared this empirical model and one based on bubble dynamics by Thorpe (1984) by interpreting continuous surface ocean oxygen measurements made by remote sensors in the Middle Atlantic Bight. While both models underpredicted the \( O_2 \) sensor data during storms, the model of Thorpe (1984) came much closer to reproducing the results. The difference between the models and their agreement with the data is probably caused by the time scales of the measurements; the paradigm produced from monthly observations was not able to reproduce results from individual storm events measured by a continuous recorder. Until more general agreement over different time scales is achieved, determination of the air injection flux from wind speed and empirically determined parameters alone will be a risky exercise.

Transport away from the euphotic zone in most mixed layer models is parameterized by vertical mixing (eddy diffusion) and advection. The diapycnal mixing parameter necessary to accomplish heat and mass balance (\(~1 \text{ cm}^2 \text{s}^{-1}\), Musgrave et al., 1988; Spitzer and Jenkins, 1989) is greater than that predicted from microstructure determinations (0.3 cm\(^2\) s\(^{-1}\) or less, e.g., Denman and Gargett, 1988). Lewis et al. (1986) argued that fluxes derived from microstructure-determined eddy diffusion coefficients were statistically the same as \(^{15}\text{NO}_3^-\) uptake experiments over a two-week period in the north Atlantic Ocean. The mean eddy diffusion coefficient was 0.4 cm\(^2\) s\(^{-1}\); however, the 95% confidence interval spanned nearly three orders of magnitude (0.007 to 2.3 cm\(^2\) s\(^{-1}\)), obscuring the meaning of these results for long-term comparisons. Large et al. (1986) concluded from an experimental study using thermister arrays that the heat balance in the upper Subantarctic Ocean during fall cooling required eddy diffusion coefficients in the seasonal thermocline of 4 cm\(^2\) s\(^{-1}\) during storms.

The necessity for values greater than a few tenths of a cm\(^2\) s\(^{-1}\) to reproduce annual nutrient and tracer data may be an artifact of interpreting episodic, multidimensional processes using a continuous one-dimensional model. Jenkins (1988) demonstrated that the entire flux of \(^{3}\)He to the upper ocean near Bermuda could be accomplished by only a few (3–5) events of the type observed only once during a two-year monthly sampling program.

Multidimensional, continuous data sets and models are required to resolve the mechanisms of nutrient transport to the euphotic zone and gas transfer at the air–water interface. Research is tending in this direction, but the effort and cost are substantial. Until mechanisms and forcings are understood, net biological oxygen production can be estimated by evaluating mixing and air–water transfer parameters using simultaneously determined inert gases with oxygen measurements (Craig and Hayward, 1987; Spitzer and Jenkins, 1989; Emerson et al., 1991).

Case studies

Stations S and P

Biological oxygen production has been estimated from data at stations S and P using measurements of inert gases and oxygen. There are sufficient interdisciplinary studies at these sites to compare net oxygen production with other net nutrient fluxes (Table 1). At Bermuda the inert gases \(^{3}\)He and argon were used to estimate gas exchange, air injection, and transport parameters. The upper limit of the net biological oxygen production determined from this study agrees with independent estimates from the \( \text{NO}_2^+\text{He} \) relationship. The value of 0.6 mol N m\(^{-2}\) yr\(^{-1}\) is roughly three times the mean particulate nitrogen flux estimated from two years of shallow (100 m) sediment trap data. Altabet (1989) suggested that one-third to one-half of the discrepancy could be relieved by accounting for the mixing of suspended particulate nitrogen out of the euphotic zone. Mixing of DON out of the upper ocean would, naturally, have the same effect.

At Station P mass balances of argon and nitrogen were used to estimate daily summertime gas exchange and air injection rates. Transport across the base of the mixed layer was assumed to be negligible during this period (Emerson et al., 1991). Mean values of the nitrogen export estimated from net summertime \( O_2 \) production are nearly half the mean calculated from depth-
90%. A possible reason for differences in this direction is that the mass balance is dominated by gas exchange and other processes would cause the A02/AN ratio to change from 9.1 to 4.41. Where this process is important, O2 and N ratios (and hence C and N ratios) in the upper ocean will be different from “Redfield” stoichiometry.

Station ALOHA

Initial results of N2, Ar, and O2 measurements at Station ALOHA are presented in Figure 2. The upper ocean in this region is characterized by a mixed layer that varies in depth from nearly 120 m in spring to less than 10 m in early summer (Fig. 2a and b). A shallow salinity maximum, which originates at the surface to the north (Seckel, 1968), exists beneath the mixed layer (Fig. 2c) and above the “18-degree” or “mode water” (Masuzawa, 1969), which has its surface origin in the frontal regions of the North Pacific (Reid, 1973; Fine et al., 1981). We identify the boundary between these two water masses to be the density horizon σθ = 25.

The oxygen profile over this depth interval (Fig. 2d) is characterized by uniform, slightly supersaturated (Table 2) waters in the mixed layer overlying the summertime shallow oxygen maximum which has its base at the 1% light level (~100 m). Oxygen concentrations decrease immediately below the euphotic zone, indicating net respiration, but the profile becomes nearly vertical at the salinity maximum mode water boundary (σθ = 25; Fig. 2d). Because the mode water is a source of high nutrients and oxygen concentrations, it appears at this location as a slight oxygen maximum at σθ ~ 26 (Winn et al., 1991). Nitrogen and argon are also slightly supersaturated in the mixed layer (Table 2), but they increase nearly monotonically with depth following the temperature decrease (Fig. 2e and f).

As a first cut at an oxygen balance, we interpret the oxygen changes in the ocean above σθ = 25. This interval represents the “locally outcropping” ocean, since the salinity maximum reaches the surface within the nutrient-depleted subtropical gyre. Import of “new” nitrate to the oligotrophic ocean comes from waters which outcrop at the frontal regions and further north with densities greater than σθ = 25. The mass balance is particularly convenient for oxygen because the region is bounded at depth by a near-zero O2-depth gradient, so the O2 concentration is relatively insensitive to diffusive fluxes from below.

The mass balance for a dissolved gas of concentration C (mol m~3), in the depth range between the surface and the depth of the σθ = 25 isopycnal, H (m), is

\[
df^\text{H}Cdz/dt = F_x - F_n + V[(C_{ml}) - [C_1]] + K(dC/dz)_H + J \tag{4}
\]

### Table 1. Comparison of net nitrogen uptake derived from oxygen mass balance in the subtropical Atlantic and subarctic Pacific with other measures of net nutrient export. Oxygen fluxes are converted to nitrogen units using A02/AN ratios in the upper pycnocline.

<table>
<thead>
<tr>
<th>Location</th>
<th>Period (units)</th>
<th>Oxygen mass balance</th>
<th>Other</th>
</tr>
</thead>
<tbody>
<tr>
<td>Subtropical</td>
<td>Annual</td>
<td>0.3-0.7* (100 m)</td>
<td>0.6*</td>
</tr>
<tr>
<td>Subarctic</td>
<td>Summer</td>
<td>1.6 ± 0.1 (70 m)</td>
<td>3.1 ± 1.3*</td>
</tr>
</tbody>
</table>

\*Spitzer and Jenkins (1989): 3-6 mol O2 m~2 yr~1 is transformed to nitrogen units assuming ΔO2/ΔN = 9.1 (Minster and Bonladhid, 1987).

\* Jenkins (1988) based on NO3-3He relationship.

Figure 2. Time-series data from Station ALOHA. (a) Temperature (°C), (b) sigma t, (c) salinity, (d) oxygen (µmol/l), (e) argon, and (f) nitrogen. The upper dashed line illustrates the mixed layer depth and the lower dashed line the depth to $\sigma_t = 25$. 
Figure 2. Continued.
Figure 2. Continued.
Thorpe (1984) created mean concentrations of both Ar suggested by Liss and Merlivat (1986) caused only a 1% speed from nearby NDBC buoys. Use of the Wannin-water exchange is scaled to monthly averaged wind change in mean concentrations of N₂, Ar, and O₂ consumption (J) is parameterized as a zero order term, J (mol m⁻² yr⁻¹). Biological oxygen production (concentration) is calculated in May and September-December. The predicted decrease in concentration after August is due to large increases in the degree of saturation in surface waters.

The inability of gas exchange and air injection to predict the mean values of N₂ and Ar in May and after August is probably caused by exchange with the deeper ocean during these periods. Increase in the eddy diffusion coefficient resolves the problem for the inert gases (Fig. 3) but has no effect on the prediction of the mean oxygen concentration because of the near zero gradient at the bottom boundary; the oxygen field above $\sigma_\theta = 25$ is independent of mixing with the ocean interior.

Rates of oxygen production necessary to explain the difference between the measurements and that predicted for an abiotic ocean are illustrated in Figure 3d. There are two peaks in production, one in spring and one in fall. The curve in Figure 3d is integrated with respect to time to derive a net biological O₂ production above the $\sigma_\theta = 25$ density horizon of 1.0 mol O₂ m⁻² yr⁻¹ (0.10 mol N m⁻² yr⁻¹). We hasten to point out that this value includes both regions of net O₂ production (the euphotic zone; 0–100 m) and net respiration (the zone immediately below it; 100–180 m). Euphotic zone production alone would be substantially greater; for this reason the result is not comparable to those in Table 1.

Sediment trap nitrogen fluxes at a depth of 150 and 300 m for the year 1990 were 0.14 ± 0.04 and ~0.07 ± 0.02 mol N m⁻² yr⁻¹ (Winn et al., 1991), indicating that the large particle transport is a sufficient mechanism to remove the nutrient flux out of the upper 175 m predicted from the O₂ mass balance. Preliminary results, however, indicate that particle transport is insufficient to account for the flux out of the euphotic zone, which is similar to the case at Bermuda (Table 1). This observation will be the subject of a future publication.
Figure 3. Results from the model calculations. (a), (b), and (c) The mean N₂, Ar, and O₂ concentration in the depth region zero meters to θ = 25 versus time in Julian days. Filled circles are measured mean values with ±1% error bars. Lines represent predictions assuming transport parameters V and K = 0 and the gas exchange/wind speed relationship of Liss and Merlivat (1986) with no air injection (dash-dot line) and that predicted by Spitzer and Jenkins (1989, solid line). Dashed lines represent the solution for K = 15 cm s⁻¹ during the last two sampling periods. (d) Net O₂ production derived from the difference between measured and predicted values in (c).
Conclusions

Net biological oxygen production derived from time-series measurements agree within a factor of three with other estimates of net nutrient flux from the euphotic zone. In the oligotrophic North Atlantic (Station S) the net annual \( \text{O}_2 \) production predicts a mean nitrogen export that exceeds mean sediment trap fluxes by roughly a factor of three. At Station P in the subarctic Pacific the mean summertime net \( \text{O}_2 \) production translates, via the \( \Delta \text{O}_2/\Delta \text{NO}_3 \) ratio, to about half the mean estimate of net nitrogen uptake from in vitro incubation studies. Particularly in the latter case, the variability about the mean calls into question the significance of the difference in the estimates. Preliminary estimates of net \( \text{O}_2 \) production at Station ALOHA north of Hawaii suggest a net \( \text{O}_2 \) production of 0.7 mol m\(^{-2}\) yr\(^{-1}\) in the upper 175 m of the ocean. As this depth interval includes the euphotic zone and the zone of net respiration immediately below, it is a lower limit for the euphotic zone production. When converted to nitrogen (0.08 mol N m\(^{-2}\) yr\(^{-1}\)) this value is more than half the mean particulate nitrogen flux measured using sediment traps by the Station ALOHA time-series scientists.

Future research toward resolving the differences in net biological fluxes from the euphotic zone using different approaches should focus on: (1) the role of mixing of dissolved and suspended particulate matter out of the euphotic zone in bridging the gap between \( \text{O}_2 \) mass balance and sediment trap particle fluxes; (2) the importance of carbon-rich DOM produced in surface waters in altering the \( \Delta \text{O}_2/\Delta \text{DIC}:\Delta \text{NO}_3 \) stoichiometry during photosynthesis and respiration from that of the particulate matter; and (3) the role of heterotrophic \( \text{NO}_3 \) uptake in nitrogen cycling and in \( ^{15}\text{N} \) incubation studies.

References