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NOTE

Importance of dissolved organic nitrogen and phosphorus to biological nutrient cycling

GEORGE A. JACKSON* and PETER M. WILLIAMS*

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Abstract—Dissolved organic nitrogen (DON) and dissolved organic phosphorus (DOP) are large and important fractions of oceanic nutrient pools, especially in euphotic zones. Their inclusion with nitrate (NO_3) and phosphate (PO_4) to form total dissolved nitrogen and total dissolved phosphate improves the Redfield argument linking organism N:P values with NO_3:PO_4 values. DON and dissolved organic carbon have minimum concentrations of about 1.3 and 30 µM, respectively, suggesting the ubiquitous occurrence of a slowly degradable, 'inert' dissolved organic component. The labile fractions of DON could be important nutrient sources in oligotrophic waters, even at degradation rates calculated to be $<0.005\ d^{-1}$.

INTRODUCTION

THE ELEGANCE of the Redfield ratios has been an inspiration to biological and chemical oceanographers since they were first published. REDFIELD (1934) showed [and later amplified in REDFIELD (1958) and REDFIELD *et al.* (1963)] that major plant nutrients, such as NO_3 and PO_4, change concentrations in seawater in a fixed stoichiometry that is the same as the N and P stoichiometry of planktonic organisms. The implication that Redfield drew was that organisms control the nutrient concentrations and their distributions.

Nitrate and phosphate are not the only forms of nitrogen and phosphorus that can be used by marine plants to satisfy their nutrient needs for growth. Other nutritional sources of nitrogen include ammonia, urea, and amino acids. DUGDALE and GOERING (1967) noted that ammonia and nitrate are supplied to the euphotic zone by different processes, with ammonia coming from recycling within the euphotic zone and nitrate coming from movement of deeper water into the euphotic zone. It has been argued frequently that within the euphotic zone ammonia is the most important nitrogen form released and taken up (EPPLEY and PETERSON, 1979); however, its concentrations are often below detection, especially in the open ocean (MCCARTHY, 1980).

Dissolved organic nitrogen and dissolved organic phosphorus compounds are a poorly characterized group; each is present in high enough concentration in surface waters so that inclusion in an index of total dissolved nitrogen and phosphorus compounds significantly changes the nutrient ratios. Our purpose in this paper is to discuss the importance of DON and DOP to the nutrient economy of the ocean by using a modified Redfield approach.

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* Institute of Marine Resources A–018, Scripps Institution of Oceanography, University of California, San Diego, La Jolla, CA 92093, U.S.A.

METHODS

All water samples for dissolved organic carbon (DOC), DON, and DOP analyses were filtered through Whatman GF/C glass fiber filters (previously ignited at 450°C) and frozen. These filtrates thus included small amounts of bacteria, picoplankton, inert particles, and colloids as well as dissolved components. DOC determinations were run in triplicate by the techniques of Menzel and Vaccaro (1964) and DON and DOP in duplicate by u.v.-oxidation (Armstrong *et al.*, 1966; Strickland and Parsons, 1972). DON as used here includes ammonia and urea. It should be noted that urea oxidation is variable (40 to 80%) by u.v. oxidation. Samples for POC and PON analyses were collected on ignited 24 mm diameter GF/C glass fiber filters and immediately frozen. The filters (single sample) were analyzed for POC and PON using a Hewlett–Packard Model 185B CHN analyzer (Karl and Holm-Hansen, 1978). Duplicate NO_3 and PO_4 and single dissolved oxygen determinations followed methods outlined in Strickland and Parsons (1972). Nitrate values include nitrite and hence are actually NO_3 + nitrite.

The analytical precision at 1s.d. for each determination in μmoles l^{-1} was: $NO_3 = \pm 0.03$; $PO_4 = \pm 0.02$; $DON = \pm 0.2$; $DOP = \pm 0.02$; and $DOC = \pm 3$. Total dissolved nitrogen (TDN) is NO_3 plus DON; total dissolved phosphorus (TDP) is PO_4 plus DOP.

RESULTS

The analytical data discussed here are derived from water samples collected over a period of 16 years throughout the Pacific Ocean (Table 1, Fig. 1). Data in Figs 3 to 8 were assembled from the profiles listed in Table 1. Two of the profiles (profiles 1 and 14), have been previously discussed (Holm-Hansen *et al.*, 1966; Williams *et al.*, 1980).

Typical results for a profile off Southern California (Fig. 2) indicate that surface concentrations of NO_3 (<0.1 μM) and PO_4 (<0.3 μM) were lower than DON (6.1 μM) or PON

Table 1. *Station positions*

Profile	Cruise/year	Station	Latitude	Longitude	Comments
1	FCRG 65/1 1965	2	33°18′N	118°40′W	San Clemente Basin
2	FCRG 66/1 1966	22	9°04′S	83°37′W	Off Peru
3	Eltanin 51 1972	1	46°S	173°W	New Zealand
4	Eltanin 51 1972	3	45°9′S	172°45′E	to
5	Eltanin 51 1972	4	59°38′S	171°11′E	Antarctica
6	Eltanin 51 1972	6	66°15′S	166°08′E	Antarctica
7	Eltanin 51 1972	7	71°32′S	171°38′E	Antarctica
8	Eltanin 51 1972	9	73°57′S	175°06′W	Antarctica
9	Eltanin 51 1972	12	76°S	159°55′W	Ross Sea
10	Eltanin 51 1972	14	77°44′S	160°04′W	Ross Sea
11	CATO I 1972		31°N	155°W	North central Pacific gyre
12	CATO II 1972	36	0°N	155°W	Equatorial Pacific
13	CATO II 1972	49	35°S	155°W	South central Pacific gyre
14	INDOPAC 1977	15	28°N	155°W	North central Pacific gyre
15	SCBS 18 1981	305	33°45′N	118°47′W	Santa Monica Basin

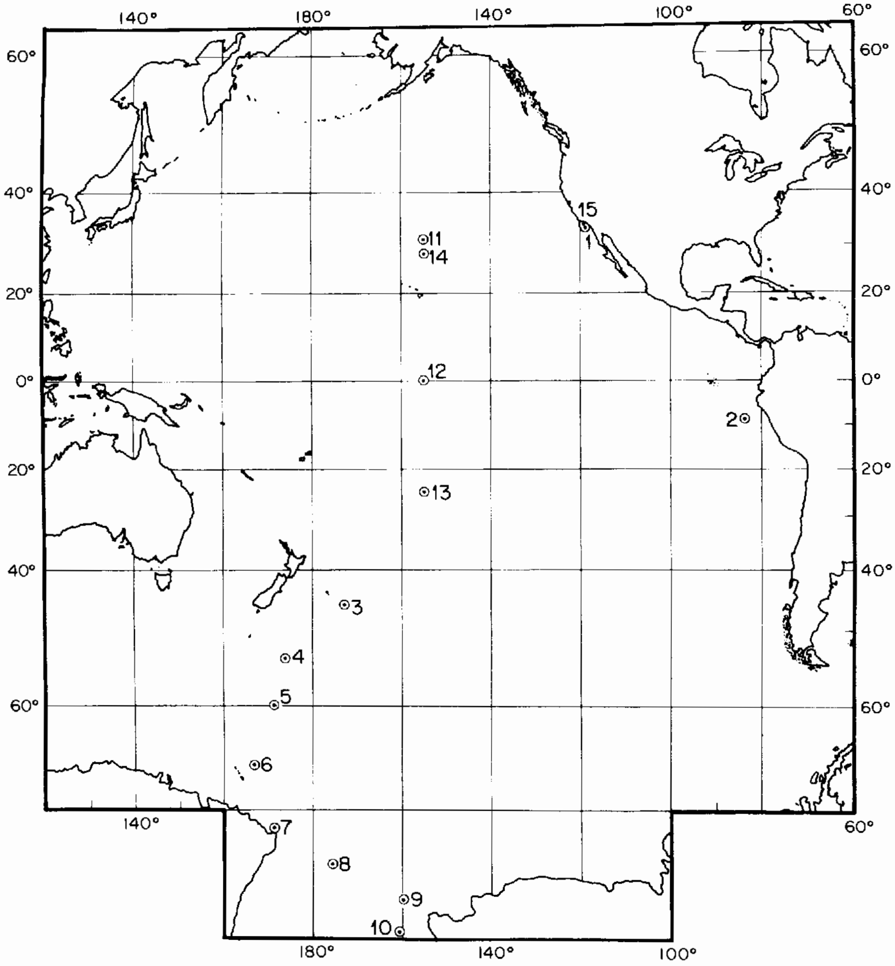

Fig. 1. Locations sampled for dissolved organics.

(0.8 μM) and about the same as DOP (0.2 μM). The contribution of DON and DOP to the total dissolved N and P in the surface mixed layer (upper 30 m) illustrates the importance of dissolved organic fractions in any accounting of nutrient dynamics.

Analysis of the original data from all the stations showed that DON and DOP concentrations were systematically highest where NO_3 and PO_4 concentrations were lowest. Nitrate concentrations were always greater than those of DON when NO_3 was >6 μM, and PO_4 concentrations were always greater than DOP concentrations when PO_4 was >0.3 μM. Thus, TDN and TDP were poorly estimated by NO_3 and PO_4 at typical surface concentrations (Fig. 3). (Note that DON concentration is the difference between TDN concentration and NO_3 concentration, or the height above the 45° line in Fig 3.) The average ratio of TDN and NO_3 changes would be given by the slope of the regression line between TDN and NO_3, 0.95 (Fig. 3). The slope for the TDP/PO_4 case was 0.99. The implication is that a typical TDN change would be about 5% less than that of NO_3 and the typical TDP change about 1% less than that of PO_4. Thus, average TDN and TDP changes were more similar to NO_3

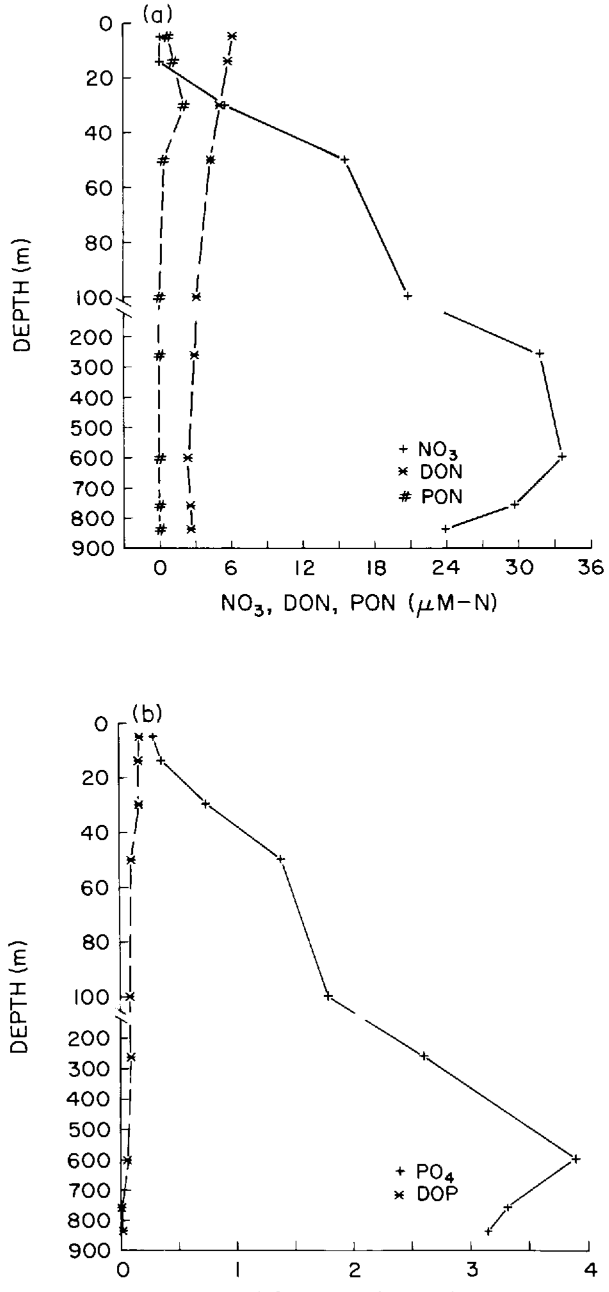
(a)
DEPTH (m)
0
20
40
60
80
100
200
300
400
500
600
700
800
900
0
6
12
18
24
30
36
NO_3, DON, PON (μM-N)
+ NO_3
× DON
PON
(b)
DEPTH (m)
0
20
40
60
80
100
200
300
400
500
600
700
800
900
0
1
2
3
4
PO_4, DOP (μM-P)
+ PO_4
× DOP

Fig. 2a, b.

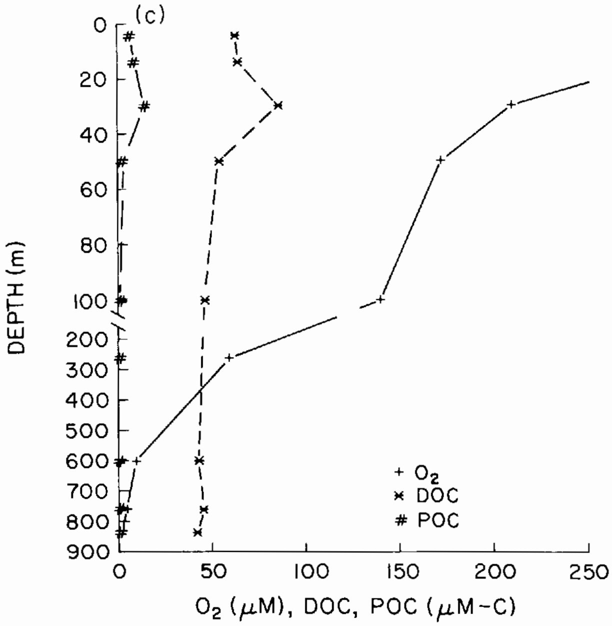

Fig. 2. Vertical distributions of nitrogen species at profile 15 off Southern California: (a) NO_3, DON, and PON; (b) PO_4 and DOP; (c) O_2, DOC, and POC. Low oxygen concentrations cause a decrease in nitrate concentrations relative to phosphate in deep waters. Bottom depth = 890 m.

and PO_4 changes than the TDN and TDP concentrations were to NO_3 and PO_4 concentrations.

The Redfield ratio for seawater is given as the slope of a regression line fit to the NO_3 vs PO_4 data, not as the ratio of the actual values. An analysis of NO_3 and PO_4 concentrations for all of our samples, deep and shallow, showed the expected classic Redfield relationship between the two (Fig. 4), with some caveats.

The first caveat is that samples from low oxygen areas, such as the deep basins off Southern California and the area off Peru, had relatively high concentrations of PO_4 relative to NO_3 because of denitrification (FIADEIRO and STRICKLAND, 1968; SHOLKOVITZ, 1972; JACKSON, 1982). High PO_4 concentrations relative to those of NO_3 were also characteristic of our samples for other areas where PO_4 concentrations were greater than about 2.5 μM. Waters high in phosphate are typically lower in oxygen (CRAIG *et al.*, 1981). The NO_3 to PO_4 slope for a least-squares-fit line fit to all data was 13.2 ($r = 0.967$). When those samples with total dissolved phosphorus (TDP) concentrations > 2.5 μM were excluded, the least-squares-fit line had a slope of 15.5. This slope was much closer to the traditional Redfield value of 16. The slope of the regression line calculated for all points had a lower value because of the NO_3 deficiency at high PO_4 concentrations. We have omitted those samples with TDP concentrations >2.5 μM in subsequent regressions unless otherwise stated. REDFIELD *et al.* (1963) effectively did this by using only samples taken at depths shallower than 1000 m in the Atlantic Ocean.

The second caveat, noted earlier by REDFIELD *et al.* (1963), is that at PO_4 concentrations <0.8 μM most NO_3 vs PO_4 values fell below the Redfield ratio regression line (Fig. 4,

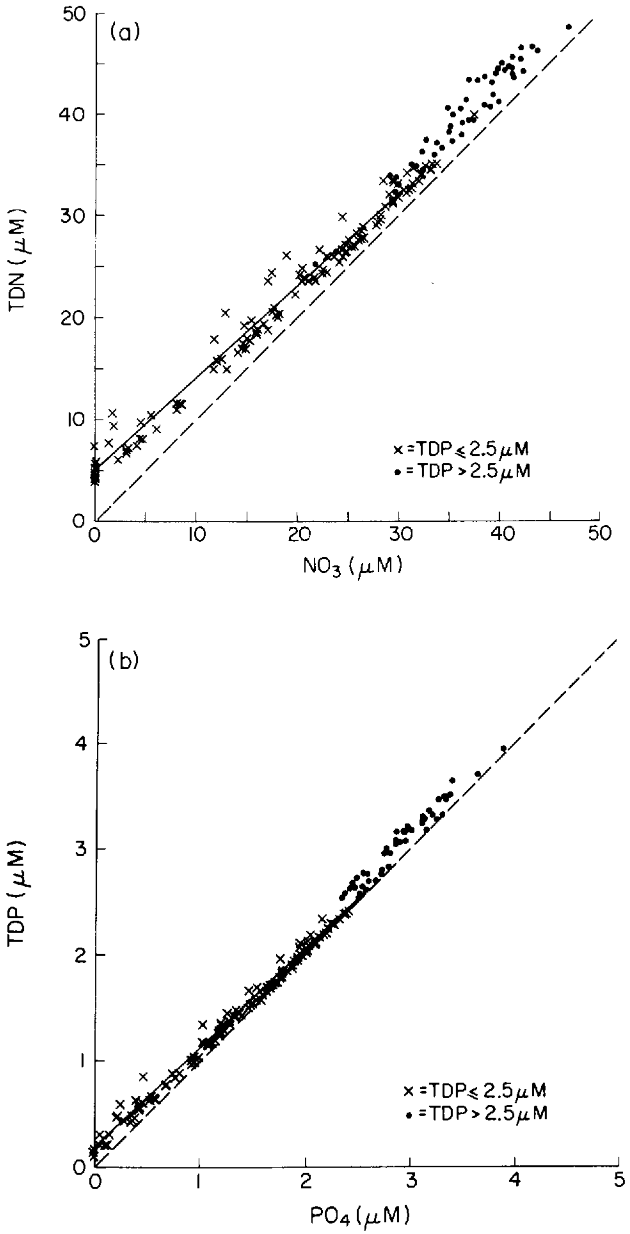

Fig. 3. TDN and TDP vs NO_3 and PO_4, respectively: (a) TDN as a function of NO_3. The least-squares fit for all points is $[TDN(\mu M)] = 0.946\ [NO_3(\mu M)] + 4.50$ ($r^2 = 0.99$, $n = 186$). The 95% confidence limits on the slope are 0.931 and 0.961. For $TDN \leqslant 2.5\ \mu M$, the fit is $[TDN(\mu M)] = 0.901\ [NO_3(\mu M)] + 5.04$ ($r^2 = 0.99$, $n = 134$); (b) TDP as a function of PO_4. The least-squares fit for all points is $[TDP(\mu M)] = 0.989\ [PO_4(\mu M)] + 0.13$ ($r^2 = 0.99$, $n = 186$). For $TDP \leqslant 2.5\ \mu M$, $[TDP(\mu M)] = 0.936\ [PO_4(\mu M)] + 0.19$ ($r^2 = 0.99$, $n = 134$). Dashed lines denote where $TDN = NO_3$ or $TDP = PO_4$.

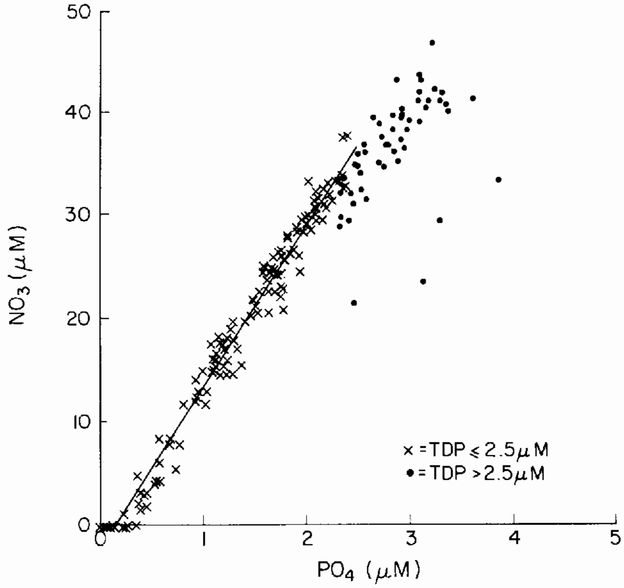

Fig. 4. Nitrate-phosphate relationship. The least-squares fit to a linear relationship for all points is $[NO_3(\mu M)] = 13.2\ [PO_4(\mu M)] + 0.23$ ($r^2 = 0.935$, $n = 186$). For samples with TDP $\leqslant 2.5\ \mu M$, the relationship is $[NO_3(\mu M)] = 15.5\ [PO_4(\mu M)] - 2.27$ ($r^2 = 0.978$, $n = 134$) (solid line).

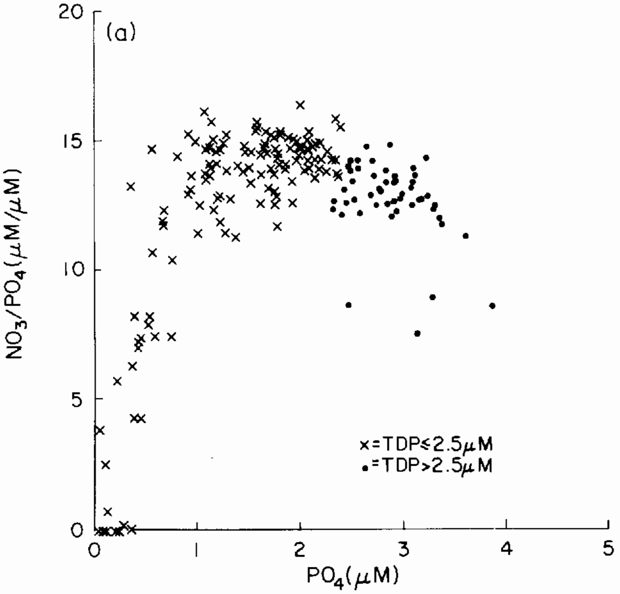

Fig. 5a.

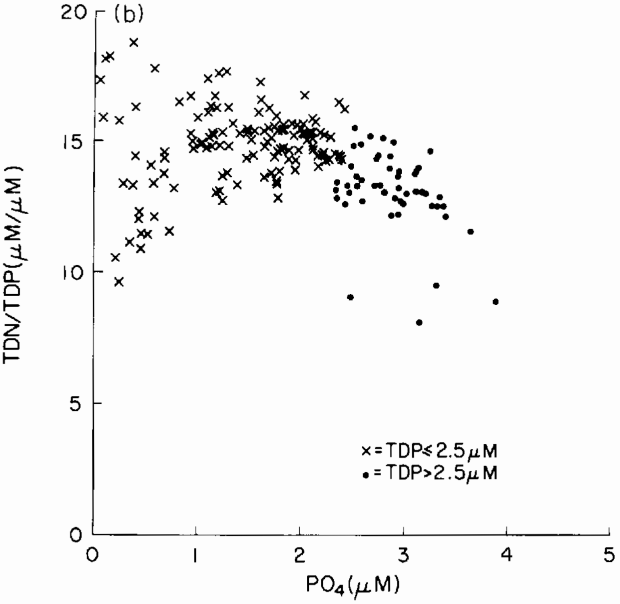

Fig. 5. Ratio of concentrations of nitrogen to phosphorus compounds as a function of phosphate concentration. (a) NO_3/PO_4. (b) TDN/TDP. Greater scatter at low concentrations could be caused by larger relative error on measurements at low concentrations.

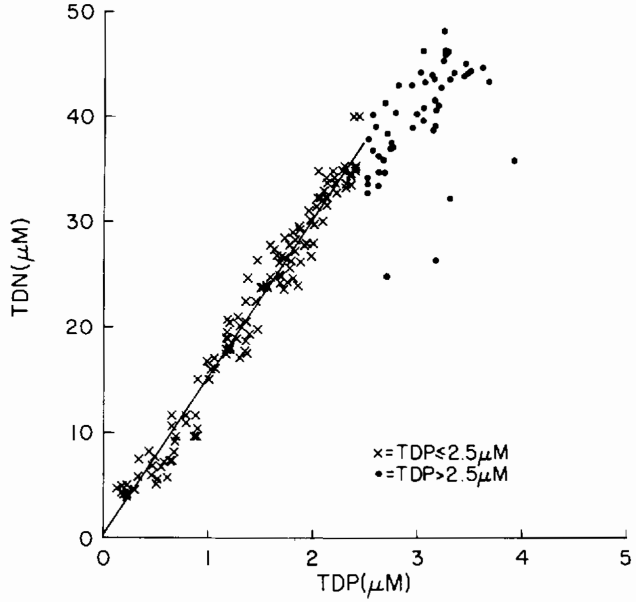

Fig. 6. Total dissolved nitrogen–total dissolved phosphorus relationship. The least-squares fit to a linear relationship for samples with TDP ≤ 2.5 μM is [TDN(μM)] = 14.96 [TDP (μM)] + 0.20 ($r^2 = 0.97$, $n = 134$). For all points, the fit is [TDN(μM)] = 12.67 [TDP (μM)] + 3.00 ($r^2 = 0.93$, $n = 186$).

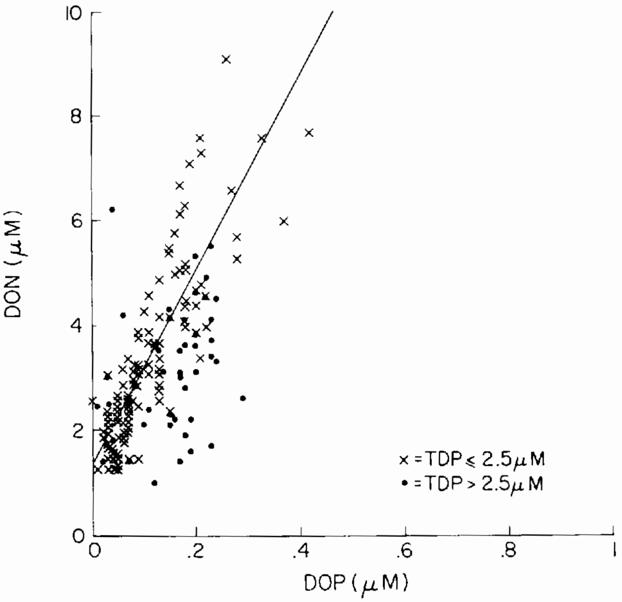

Fig. 7. Dissolved organic nitrogen–dissolved organic phosphorus relationship. The least-squares fit to a linear relationship for samples with total dissolved phosphate ≤2.5 μM is [DON(μM)] = 18.39 [DOP(μM)] + 1.36 ($r^2 = 0.73$, $n = 134$).

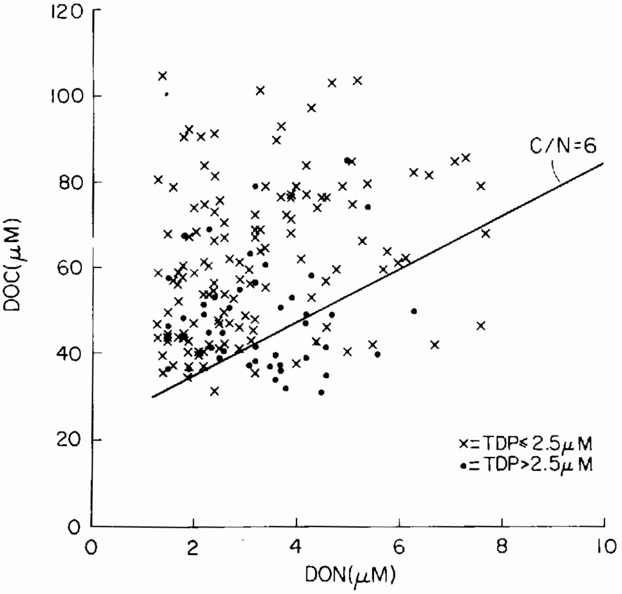

Fig. 8. Dissolved organic carbon–dissolved organic nitrogen relationship. Line with slope 6 is drawn as representative of biological organisms. Minimum concentration of DOC is about 30 μM and of DON about 1.3 μM. Note that the line does not go through the origin but does go through the point of minimum DOC, minimum DON concentration.

slope = 15.5). These deviations from the Redfield ratio were particularly striking when plotted as the ratio of NO_3 to PO_4 (Fig. 5a). Most NO_3:PO_4 values were <12 when PO_4 concentrations were less than about 0.8 μM. The ratio of TDN to TDP was less variable at these low PO_4 concentrations (Fig. 5b).

The relationship between TDN and TDP (Fig. 6) was different than that between NO_3 and PO_4 (Fig. 4). The slope for a linear regression of TDN vs TDP was 15.0 rather than the NO_3 vs PO_4 slope of 15.5. Differences between slopes were statistically significant at the 0.06 level. *Y*-intercepts of the two lines, 0.10 μM for TDN and −2.4 μM for the NO_3, were significantly different at the 0.05 level.

DON and DOP concentrations were also linearly related (Fig. 7). The slope of the linear regression curve fit was 18.7. This slope for the DON to DOP relationship was significantly different from that of nitrate to phosphate at the 0.06 level.

DOC and DON concentrations showed little relationship (Fig. 8). DOC and DON minimum concentrations were about 30 and 1.2 μM, respectively. These values represent relatively 'inert' background concentrations of dissolved organic matter with a C:N value of 25 on which were superimposed variable concentrations of more labile organic matter. This inert fraction contained, on average, about 80% of the DOC and 30% of the DON in deep-ocean waters.

DISCUSSION

Distribution of DON previously has been associated with phytoplankton production (DUURSMA, 1961; FRAGA, 1966; HOLM-HANSEN *et al.*, 1966; WHITLEDGE, 1981). The upwelling area off Peru, where DON reaches 10 μM and ammonia and urea 4 μM represents an extreme case (WHITLEDGE, 1981). Additionally, an inverse relationship between DON and NO_3 concentrations has been noted (BANOUB and WILLIAMS, 1972; BUTLER *et al.*, 1979). BUTLER *et al.* (1979) reported values of DON:DOP (25 to 42) and TDN:TDP (17 to 24) for the English Channel, which are considerably higher than our average value of 15. Salinity distributions in the English Channel show some influence of river input (ARMSTRONG *et al.*, 1970, 1974) which may effect dissolved organic matter in the same way that it did off Georgia (GARDNER and STEPHENS, 1978). Whatever the reasons for the differences among these studies, our results do support the above conclusions that DON and DOP production are part of euphotic zone processes and that DON and DOP concentrations increase as NO_3 and PO_4 concentrations decrease.

Properties of DON and DOP

STRICKLAND *et al.* (1969) observed a DON change of 1.2 μM over 4 days for a large (7×10^5 l) diatom culture and a DON change of 3 μM over 3 days for a similar dinoflagellate culture. The minimum DON concentration measured was 4.0 μM under nutrient-depleted conditions. The nitrogen budget for these systems balanced only when DON was included.

THOMAS *et al.* (1971) attempted to grow phytoplankton in near-surface water from the eastern tropical Pacific Ocean using naturally occurring DON as the nitrogen source. Because the phytoplankton did not grow during 4 to 5 day incubation periods in this water (THOMAS, 1969), which was low in NO_3 (<0.1 μM) but contained as much as 13 μM DON, they concluded that the DON was inert. THOMAS *et al.* (1971) did suggest that the DON measured by STRICKLAND *et al.* (1969) was not inert.

The nutritive properties of DON depend on the chemical composition of this pool. Urea, the major component of DON readily utilized by phytoplankton, typically has a concentration range of 0 to 0.5 μM (0 to 1 μM of urea–N) in surface waters (EPPLEY *et al.*, 1977; BUTLER *et al.*, 1979; MCCARTHY, 1980) and is normally undetectable below 100 m. The concentrations of dissolved free and combined amino acids, the other major labile components of DON which have been identified, vary from 2 to 200 nM in deep water and 20 to 600 nM in surface waters (LEE and BADA, 1977; MOPPER and LINDROTH, 1982; P. M. WILLIAMS, unpublished results for Southern California Bight). Thus, the total labile organic nitrogen identified to date represents only 5 to 20% of the total DON normally present in seawater. It is evident from Fig. 8 that DOC and DON show no simple C:N relationship, and that in most of our samples C:N molar ratios were greater than those of planktonic organic matter (4 to 8), amino acids and proteins (2 to 6), amino sugars (6), or urea (0.5). Low organic C:N ratios (<6) in surface and/or deep seawaters have been reported by earlier workers (WILLIAMS, 1975, for summary). The low ratios are due primarily to the type of analysis, i.e., DON concentrations by dry combustion DON analyses are higher than those measured by the u.v. oxidation technique used in this work. The wide range in C:N values for dissolved organic matter implies that it has a variable molecular composition such that turnover rates and biological interactions should vary with the specific compound present.

The vertical distribution of DON, with concentrations high near the surface and decreasing with depth, implies that DON is produced by organisms as part of the euphotic zone nutrient cycle and that it is degraded by organisms, primarily bacteria, in deeper waters. The existence of spatial concentration gradients allows mixing processes to transport chemical substances from high to low concentration locales. Mixing could transport fast reacting DON in the euphotic zone upward at rates greater than for NO_3 if the DON vertical concentration gradient were greater for the DON. Alternatively, decreasing DON and increasing NO_3 concentrations with depth would cause vertical mixing to both add to, and remove nitrogen from, the euphotic zone. The relative transport rate of the two processes depends on the ratio of the DON and NO_3 gradients for a Fickian process. The relationship between TDN and NO_3 was such that, on average, a change in TDN was only 90% of a change in NO_3 (Fig. 3). This implies that the average TDN gradient is 90% of the NO_3 gradient and that 10% of 'new nitrogen' entering the euphotic zone by mixing of NO_3 is lost by DON flux and 90% by particle settling (DUGDALE and GOERING, 1969).

It is possible to calculate how long it would take to accumulate given levels of DON if all the nitrogen used in phytoplankton production were converted to DON or, equivalently, how long it would take to deplete the reactive DON pool if it served as the sole nitrogen source for phytoplankton growth. This minimal turnover time is equal to the reactive DON concentration divided by the nitrogen assimilation rate where the nitrogen assimilation rate is estimated by multiplying the measured carbon assimilation rate by 1/6 (the N:C value for phytoplankton, REDFIELD *et al.*, 1963).

In the oligotrophic Central North Pacific Gyre (CATO I, profile 11, Fig. 1), NO_3 and PO_4 concentrations in the euphotic zone were <0.02 μM, average DON was 4.5 μM, and measured productivity was 1.07 μg C l^{-1} d^{-1} (EPPLEY *et al.*, 1977). These values give a nitrogen assimilation rate of 15 nM d^{-1} and a minimal DON turnover time of 303 days if all DON is used, or 215 days if 1.3 μM of the DON is inert. A conversion rate of 0.005 d^{-1} of labile DON is enough to meet all the nitrogen needs of phytoplankton in the gyre.

In the Southern California Bight (SCBS 305, profile 15, Fig. 1), NO_3 and PO_4 were 0.03 and 0.29 μM, DON was 6.14 μM, and carbon productivity was 21 μg C l^{-1} d^{-1}. This results in a calculated nitrogen assimilation rate of 0.29 nM d^{-1} and a minimal turnover time of 21 days for total DON and 17 days if inert DON is excluded. Thus, the turnover of DON potentially could be 13 to 14 times faster in this coastal water than in the Central North Pacific Gyre.

Similar calculations for DOP using a C:P value of 106 result in a DOP turnover time of 18 days for CATO I (DOP = 0.18 μM) and 0.86 days at SCBS 305 (DOP = 0.17 μM). This more rapid turnover of DOP compared to DON results from a smaller and more labile DOP pool.

The maximum DON turnover rates have been calculated assuming that DON and DOP are the sole N and P sources for plant growth. In fact, most of the nutrients come from N and P recycled between plants, animals, and bacteria without entering and leaving the dissolved organic pools. Because some of the nutrients involved in this cycle leave the euphotic zone in falling particles, there must be a renewal from other sources if the system is to maintain itself. Ultimately, this renewal is by transport of NO_3 and PO_4 into the euphotic zone. However, the large sizes of the DON and DOP pools may allow them to act as buffers during periods between infusions of NO_3 and PO_4 into the euphotic zone. If so, DON and DOP degradation rates would be slower than their maximal calculated turnover rates; yet these organic N and P pools could still be an important part of the nutrient system. Because of the slow DON degradation and/or formation rates in areas like the North Pacific Gyre validation of DON utilization by experimental rate determinations will be extremely difficult.

CONCLUSIONS

Any attempt to budget and follow the pathways of total nitrogen and total phosphorus in a euphotic zone ecostystem must account for DON and DOP transformations. Inclusion of DON and DOP in the dissolved nutrient pools is especially relevant to understanding nitrogen and phosphorus distributions in low nutrient surface waters. We suggest that the labile fraction of DON and DOP, directly or indirectly, are important sources of nitrogen and phosphorus for phytoplankton in oligotrophic ocean areas.

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