Variable Relationships of DOC with Oxygen in the Northwestern Indian Ocean and their Ecological Implications

by
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With 4 Figures and 4 Tables

Contents

Abstract	
1. Introduction	
2. Material and Methods	
3. Results and Discussion	
Acknowledgements	
References	

Abstract

The relationships between DOC and AOU in the northwestern Indian Ocean show regional variations reflecting the different biological characteristics dominating the respective zones, resulting in the variable percentages of DOM respiration through nitrate remineralisation and oxygen consumption. Carbon oxidation by denitrification is very significant in the northern Arabian Sea whereas chemolithotrophic nitrification might contribute to some extent for carbon accumulation in the south. The northern Arabian Sea characterized by the reducing environment, is found to outflux CO₂ much faster than the other regions. Considering the latitudinally variable relationships of DOC with oxidants, its different transport pathways in the water column are discussed.

1. Introduction

Oceanic dissolved organic matter contains more carbon (DOC) than the combined aquatic and terrestrial biospheres and thus this pool of DOC in the oceans forms a major reservoir in the global carbon cycle (Hunt, 1972; Hedges, 1987). Despite the importance of DOC in the biogeochemical cycling and flux of essential elements in the ocean, considerable uncertainty still exists in the amount and nature of this important carbon pool. For a detailed treatment of the subject see Marine Chemistry, 41, No. 1–3 (1993). We have recently reported on the distribution of DOC in the northwestern Indian Ocean with accent on the relationship of DOC and AOU (Kumar et al., 1990). Here we discuss the factors controlling regional differences in these relationships and their ecological implications.

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2. Material and Methods

The samplings were carried out at 20 stations on board RV SONNE during cruise 42 as part of the INDO-FRG Joint Oceanographic Programme. The detailed methods of sampling and analysis were given elsewhere (Kumar et al., 1990). However, the data collected at three stations (1) Station 8 at 20°54'N and 63°07'E (2) Station 2 at 15°31'N and 68°46'E and (3) Station 20 at 00°37'N and 56°54'E, representing north, central and southern Arabian Sea regions (Fig. 1), respectively, are analysed in detail for the present study. TCO₂ were computed from pH and titrimetric measurements of alkalinity where Gripenberg's back titration method was employed, while DOC was measured using a high temperature catalytic oxidation method with a Carlo Erba analyser using a Hastelloy C reactor with copper and cobalt oxides as catalysts. The microbiological studies carried out in ORV SAGAR KANYA are also presented in this paper. For microbial isolation, water sampling was done using either J-2 bacteriological samplers or Niskin sterile bag sampler (General Oceanics Inc., U.S.A.). For enumeration of total viable heterotrophic bacteria, membrane filtration technique was followed. Aliquots of 2 to 10 ml of samples were filtered through 0.22 um membrane filters (Millipore Inc., U.S.A.) and the filters were placed on SWC agar (Rheinheimer, 1977). Total colony forming units (TCU) were counted after incubating the plates at 25 - 28°C for 3 days. Heterotrophic activity measurements were made following the methods of Hobbie and Crawford (1969) and Harrison et al. (1971) using the uptake kinetics of ¹⁴C labelled glucose.

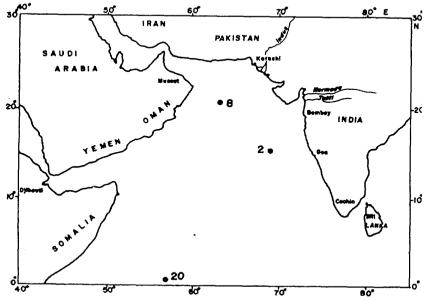


Fig. 1: Station locations in the Arabian Sea.

3. Results and Discussion

The nature of DOC might depend on the types of organisms present in an aquatic body wherein some might produce predominantly microbially degradable organic compounds, perhaps in high productivity zones, having faster and greater turnover. Our results from studies in the northwestern Indian Ocean (Kumar et al., 1990) prove the microbial oxidisability of DOC while showing the insufficiency of available oxygen and consequent nitrate consumption as an oxidant. This area experiences highly variable biological productivity patterns, having a maximum in the north and minimum in the south, together with significant horizontal patchiness (Qasim, 1982). Figure 2 depicts the decreasing DOC concentrations northward almost in all depths but with enhancing nitrate deficit (Delta N) in the intermediate layers. There is a general inverse trend between DOC and Delta N, which reveals high microbial oxidation of DOC at places of very high denitrification. The distribution of bacterial counts from 0 to 25°N (Tab. 1) shows higher bacterial biomass in the region north of 15°N at the depth upto 1000 m, especially in the area 20 - 25°N where the denitrification process predominantly occurs. On the contrary, the heterotrophic uptake of ¹⁴C glucose by the water column bacterial population (V_{max}) is found to decrease from 15°N to 25°N (Tab. 2). There is also a latitudinal variation in the turnover time. The intensity of bacterial activity and its effect on DOC oxidative consumption and denitrification are also evident through the distribution of total carbon dioxide (TCO₂) and AOU (Fig. 2). While AOU reached a maximum of 250 µmol dm⁻³ in the north and central parts, its maximum in the south is less than 200 µmol dm³. Conspicuously, figure 2 reveals the denitrification occurence, indicated by a positive nitrate deficit, only when the oxygen consumption reaches near maximum, particularly at the northern station. On the

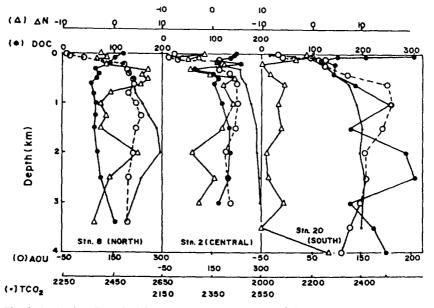


Fig. 2: Vertical profiles of DOC, AOU and Delta N (µmol dm⁻³) in the Arabian Sea.

Table1: Mean values of total viable counts of bacteria (CFU No. x 10³ l⁻¹) in different sections of the Arabian Sea

Depth m	0 – 5°N (10 stations)	5 – 10°N (11 stations)	10 – 15°N (13 stations)	15 – 20°N (11 stations)	20 - 25°N (8 stations)
1	12.7	18.0	8.7	26.0	280.0
10	8.0	_	_	40.0	194.0
20	-	_	11.0	_	294.0
50	-	23.4	_	26.0	402.0
75		28.6	19.2	_	-
100	6.0	8.8	6.4	4.0	99.0
200	5.2	3.4	2.6	3.0	4.0
300	_	_	~	3.0	2.0
500	2.5	0.3	_	2.0	1.2
1000	0.7	_	_		-

contrary the probable predominance of nitrification is implicitely inferred through exceedingly negative Delta N values in the southern Arabian Sea (Fig. 2). This seems to occur with accumulating DOC probably due to a decrease in heterotrophic bacterial populations in the south (Tab. 1). However, the gradual antagonistic changes in DOC and nitrate deficit (Delta N) seem to have reached a steady state in central part where DOC increases with depth, within the positive Delta N depth range, along with that of Delta N juxtaposed by maximum AOU values. The southward increase in DOC with only moderate oxygen consumption values (150 - 180 µmol dm⁻³) were observed with simultaneous decrease in total bacterial counts but with a proportionally higher DOC oxidation and nitrate deficits within the denitrification zone of the northern Arabian Sea. The biomass of bacteria is maximum in the north (upto 402 x 103 CFU l-1) with relatively higher DOC oxidation but minimum bacterial biomass in the south (upto 28 x 103 CFU l⁻¹) with a higher DOC pool. The observations in the northern Arabian Sea of higher bacterial biomass and faster rate of recycling support the views of Ducklow et al. (1986) that the bacterioplankton can be a sink for carbon in the planktonic food web, oxidising the DOM into CO₂.

Table 2: Heterotrophic uptake of ¹⁴C glucose by the water column microbial assemblages in the Arabian Sea

Latitude	Heterotrophic activity V_{max} (µg C I^{-1} h^{-1})	Turnover time T _t (hr)	
15°N	0.7976	30.25	
16°N	0.4315	152.65	
17°N	0.3952	657.64	
18°N	0.1001	1362.85	
19°N	0.0512	852.55	
20°N	0.0315	733.19	
21°N	0.0325	935.62	

Vertical distribution of DOC (Fig. 2) shows that there is a marked mid-depth (800 - 1000 m) increase in DOC at Station 20 whereas this is absent in the northern Arabian Sea. This increase could be due to horizontal advection or in situ production. The increased DOC in the south might facilitate the formation of bacterio-particulate aggregates which in turn may result in the bacterial chemolithotrophic production in these intermediate waters, as shown earlier by Karl et al. (1984). The negative Delta N observed below 200 m and the complete absence of positive Delta N at this Station suggests that chemolithotrophic nitrification could be a dominant process in the southern Arabian Sea.

The north-south variations in the distribution of DOC, AOU, TCO, and nitrate anomalies clearly reflect the patterns of primary productivity in the Arabian Sea, which shows a great difference between these two regions, north being highly productive. In the southern Arabian Sea (0 - 10°N) the range in productivity is found to vary from 0.33 to 676 mg C m⁻² d⁻¹ whereas it ranges between 109 and 2665 mg C m⁻² d⁻¹ in the northern Arabian Sea (Radhakrishna et al., 1978; Qasim, 1982). With a decrease in productivity, there is a marked decrease in the heterotrophic bacterial numbers in the south (Tab. 1). Furthermore, the ratio between the number of denitrifying bacteria and the nitrate reducing bacteria was found to decrease from north to south both at surface (from 0.55 to 0.03) and at 300 m (from 0.12 to 0.01) in the Arabian Sea (Loka Bharathi et al., 1988). These microbes being facultative lithotrophs or mixotrophs, their rates of activity are influenced to a greater extent by the DOC content in the environment. Our present estimations also suggest that there exists a north-south difference in the phytoplankton growth rate. Chlorophyll a specific photosynthetic rate, namely productivity per unit Chl a (calculated using integrated photic zone values) is an index of mean photic zone growth rate of phytoplankton biomass (Malone, 1977). Table 3

Table 3: Latitudinal variation of growth rate of phytoplankton biomass in the Arabian Sea

Latitude	Chl a specific pho rate (g C (g Ch	Number of stations	
	Range	Mean	Sidirono
00 - 05°N	15.2 39.4	26.8	5
$05 - 10^{\circ}N$	5.3 - 45.5	28.3	9
10 - 15°N	9.9 ~ 70.0	36.9	13
$15-20^{\circ}N$	12.9 - 168.6	58.8	14
20 - 25°N	34.8 - 110.0	61.5	14

shows the mean values for Chl a specific productivity for 5° latitudinal intervals from equator to 25° N calculated from data of Anton Bruun Cruises between 60° E and 70° E (Babenard and Krey, 1974). These values clearly indicate a lower growth rate in the south (26.8 g C (g Chl a)⁻¹ d⁻¹) whereas the northern Arabian Sea (20 - 25° N) showed a high rate of 61.5 g C (g Chl a)⁻¹ d⁻¹. However, the Chl a specific photosynthetic rates calculated from the recent estimations (Dr. P.M.A. Bhattathiri, personal communication) indicate that the southern Arabian Sea shows a range of variation between 20 and 65 g C (g Chl a)⁻¹ d⁻¹ (mean 42) near the equator and a

wider variation between 23 and 154 g C (g Chl a)⁻¹ d⁻¹ (mean 59) in the Arabian Sea north of 15°N.

The distribution of surface pigment during the winter monsoons of 78 - 79 and 79 - 80 exhibits marked differences in both the magnitude and timing of maxima within various areas of the Arabian Sea north of 10°N (Banse and McClain, 1986). The surface pigment concentrations within the mixed layer, as summarised earlier by Banse (1987) and the recent DARWIN winter survey (Bauer et al., 1991) indicate that north of 20°N, values range from 0.2 to 0.4 mg m⁻³ and further south, between 15 and 20°N, maximum surface concentrations are approximately 0.1 - 0.2 mg m⁻³. All our observations, in addition to the above seem to indicate two distinct biological processes, dominating in the two regions of the Arabian Sea; for example, the highly productive northern region is microbially active with effective DOC oxidation, including through the denitrification process. The seasonal responses in mixed-layer depth, vertical velocities due to Ekman flux divergence and the chlorophyll a distributions observed during the Monsoon Arabian Sea Air-Sea Interaction (MASAI) cruises suggest that the physical forcing is the primary factor influencing the spatial pattern of mixed-layer depth and pigment biomass during the monsoon season in the Arabian Sea (Bauer et al., 1991). They have shown that the combination of upwelling and surface layer deepening leads to latitudinal gradients in phytoplankton biomass. The latitudinal variations in chlorophyll a specific productivity, microbial biomass and the heterotrophic activity and the distribution of DOC reported in this paper also indicate the importance of the physical forcing in regulating the various biogeochemical processes. The physical processes such as the seasonal upwelling in the western Arabian Sea, monsoonally forced Ekman dynamics and the monsoonal reversal of the circulation pattern in the surface layers might help to maintain the north-south variabilities or gradients in the Arabian Sea triggered by various chemical and biological processes during most of the seasons of the year.

Detailed spatial variations in the DOC-AOU relationships are depicted in figure 3. A single straight line with an inverse relation of DOC with oxygen (Fig. 3a), for deeper as well as surface layers together, shows that there is a DOC loss due to biological oxidation in the northern Arabian Sea. However, there is an intense DOC accumulation in the deeper layers (below 150 m) of the southern Arabian Sea (Fig. 3c), which is shown by a positive relation. The single relation found for the north, with a slope (Delta AOU/Delta DOC) of -4.90 (Tab. 4) indicates that there is far more oxygen being utilized than DOC can account for in the deep sea. The observed slope is very different from the theoretical Redfield ratio. Though Sugimura and Suzuki (1988) found a single, linear relationship with a slope of 0.9 which is very close to the theoretical slope (Delta AOU/Delta DOC being 1.3), Druffel et al. (1989) found a slope of 4.8 for deeper waters. A single, linear relationship for both surface and deeper layer (correlation coefficient is -0.94) found in the northern Arabian Sea shows a strong tendency for faster recycling of DOC, probably of low molecular weight. Phytoplankton exudates, mostly of low molecular weight and probably greater in quantity due to high primary production, might contribute to the easily oxidizable DOC in the northern Arabian Sea, where a higher amount of CO₂ is produced from organic decomposition. In contrast, the deeper layers of both the central and southern Arabian Sea (Fig. 3) show positive relations (slopes 0.35 and 0.52 respectively, Tab. 4) indicating that there is an accumulation of DOC due either to a slow rate of oxidation or in situ production of DOC. Though

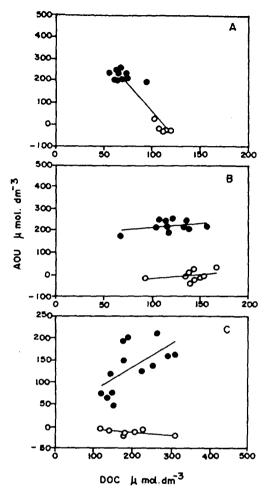


Fig. 3: The relationships between DOC and AOU in the northern (A), central (B) and southern (C) Arabian Sea. Symbols are: hollow (surface < 150 m) and solid (deep > 150 m).

oxygen consumption in the deeper layers of Station 20 is of the same magnitude as compared to the northern station (Tab. 4), DOC increases in deeper layers showing the maximum of 310 µmol dm⁻³. These observations and the conclusion are further supported by the existence of a significant variation in J/W (Production rate parameter for DOC) between -47 and +84 calculated for the different stations in the Arabian Sea (Kumar et al., 1990). The negative J/W values in the northern region (meaning a depletion of DOC) again confirm the in situ oxidation and consumption of DOC in the denitrification dominant region, whereas the positive J/W i.e. +84 (meaning an addition of DOC) in the southern Arabian Sea is due to the excess DOC addition and/or its accumulation.

Table 4: Range of variation in DOC, AOU and regression parameters

Stations	Range of variation in DOC AOU pmol dm ⁻³ pmol dm ⁻³		Regression parameters for DOC-AOU relationships	
Station 8				
Upper 150 m	102 - 119	-57 to 28	AOU = 547.9 - 4.9 DOC	
Deeper layers	55 - 94	203 to 262	AUU = 347.9 – 4.9 DUC	
Station 2				
Upper 150 m	92 – 166	-38 to 31	AOU = -61.5 + 0.40 DOC	
Deeper layers	67 – 156	175 to 257	AOU = 182 + 0.35 DOC	
Station 20				
Upper 150 m	115 - 309	-22 to - 6	AOU = -1.82 - 0.06 DOC	
Deeper layers	120 - 310	47 to 223	AOU = 29.07 + 0.52 DOC	

Particle bound bacteria are thought to be important in the remineralization of particulate organic matter (POM) while DOM flux occurs mainly into free living bacteria (Azam and Hodson, 1977). POM is not normally used by bacteria directly, and they can take up only DOM since they are osmotrophs. However, particle attached bacteria, by their exoenzymatic activity, solubilise much more than they take up for their own metabolism and growth and thus the colonised particles would become the loci of DOM release, that is available only to bacterioplankton (Azam, 1986). The observations presented in figures 2 and 3 and the data on microbial biomass (Tab. 1) show that the northern Arabian Sea might present a similar situation, where the bacterioplankton plays a major role. High primary production facilitates the production of organically rich particles that might be colonized by bacteria, leading to DOM release and further biodegradation. The high rate of decomposition in the north, as suggested by a high value for Delta AOU/Delta DOC (Tab. 4), is also reflected in the higher value of TCO₂ in the north at all depths than the corresponding ones in the central or southern Arabian Sea (Fig. 2).

Populations dominated by diatoms characteristically release a low percentage of their primary production as DOC (Lancelot and Billen, 1985). This also could be one of the reasons for low DOC in the northern Arabian Sea, where the photic growth rate of phytoplankton population is higher (Tab. 3). Lancelot and Billen (1985) in their review quoted several studies reporting a higher percentage of release by organisms under low nutrient conditions. The southern Arabian Sea always experiences relatively lower nutrient concentrations at all depths than the corresponding depths in north (Wyrtki, 1971). This sort of low nutrient, oligotrophic conditions that prevail in oceanic regions such as the southern Arabian Sea could result in higher amount of DOC. Figure 3c shows the increase in DOC even up to 310 µmol dm⁻³ in deeper waters with an increase in AOU (upto 220 µmol dm⁻³) and thus clearly indicates the accumulation of DOC, with no immediate oxidation. The southern Arabian Sea, with low bacterial biomass, probably with a dominance of the "grazing food web", might experience higher amount of DOC that persists longer in the environment. The deeper layers of the central Arabian Sea, though showing the same trend (Fig. 3b), experience a slow rate of accumulation even with an increased amount of oxygen utilization (190 to 280 µmol dm⁻³ of AOU). The concentration of DOC in the central and northern Arabian Sea is almost half of that present in southern Arabian Sea waters (Tab. 4). These contrasting relationships existing between DOC and oxygen in the Arabian Sea suggest two biologically distinct regions. The northern Arabian Sea with higher nutrient conditions, high phytoplankton production and high microbial activity shows low amount of DOC that may probably be of microbially labile compounds, whereas the southern Arabian Sea with low nutrient conditions and low phytoplankton production shows a high DOC content that may be the resultant of the production/selective accumulation of microbially refractory compounds. The regionally contrasting relationships of DOC with oxygen in the Arabian Sca perhaps indicate the variation in the degree of active condensed - DOM formation and the net DOM destruction probably triggered by the availability of phytoplankton and animal exudates. A detailed future study of the characteristics of DOM in this region would provide more insight to test the validity of the above assumption. The DOC-AOU relations for surface layers are also different regionally, wherein these points together with values for deeper waters yield negative relationship in the north, but fall into separate groups in the central and southern regions (Fig. 3).

The existence of two different processes regulating the DOC dynamics in the Arabian Sac is also shown in figure 4. The southern Arabian Sea, showing high values of DOC, experiences a negative Delta N, thus implying the dominance of nitrification whereas low DOC values and an increased and positive Delta N in the northern and central regions prove the prevalence of denitrification. The variable relationships of DOC and AOU found in the Arabian Sea in different regions imply the following four different major pathways of transfer of DOC, one or more dominating the other, in the pelagic system: (1) DOC oxidation by microorganisms, which act as remineralisers to produce the CO₂ in the water column (Ducklow et al., 1986), as found in the northern Arabian Sea. (2) DOC incorporation into the POC pool by heterotrophic uptake of DOC

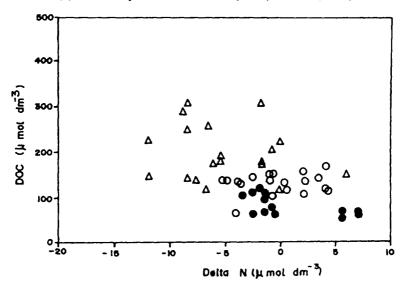


Fig. 4: Variation of DOC with respect to nitrate anomaly in the northern (filled circles), central (circles) and southern (triangles) Arabian Sea.

by free living bacteria (Paerl, 1974). The phenomenon of microbial synthesis of macroparticulate matter could be the major pathway by which carbon and energy is transferred from the micro to the macro food webs in the aquatic ecosystems (Biddanda, 1985). (3) Chemosynthetic production of DOM from dissolved inorganic carbon as suggested by Karl et al. (1984) which may be the process observed in the southern Arabian Sea. (4) Bacteria may be effective competiters with particle-feeders (including herbivores) by solubilising POM to convert it to DOM (Azam and Ammerman, 1984).

The production of DOC either by the chemosynthetic process or by a grazing dominated food web, and the resultant decreased DOC oxidation southward result in its accumulation by 150 - 200 μ mol dm⁻³ near the equator, compared to that at 21°N latitude. This in all probability resulted in the TCO₂ decrease by a similar magnitude from north to south (Fig. 2) and the piston velocities (for CO₂ outflux to the atmosphere) depend on the gradient in TCO₂ profiles and will be maximum in the north. Using our TCO₂ and pCO₂ values and having a Revelle factor of 10.0 (Takahashi et al., 1980), the evaluated f_{air} of the carbon dioxide

$$f_{air} = CO_2 (air)/(CO_2(air)+CO_2(water))$$

for the upper 100 m of this part of the Indian Ocean amounted to 0.65 at the equator and 0.81 at 21°N. Thus the CO₂ content in air over the northern part should be relatively higher than that over the southern part due to the relative difference in CO₂ outfluxes from sea water between these areas. A methane profile at 21°N in this area indicated the possibility of its atmospheric input having a concentration four times greater at 100 m depth compared to that at surface (RV SONNE 42, Cruise Report, 1986). This emphasizes the climatological significance of the high productivity areas in the oceans, especially those experiencing highly reducing conditions such as those found in the northern Arabian Sea, in emanating the greenhouse gases such as carbon dioxide and methane into the atmosphere.

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