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Supply and consumption of dissolved organic phosphorus across the subtropical Indian Ocean

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Abstract

The Indian Ocean is an understudied region for marine phosphorus (P) biogeochemistry. Emerging evidence indicates marine phytoplankton can adapt to decreasing supplies of inorganic P, a required nutrient for growth, by alternatively utilizing organic forms of P. Here we investigate the dissolved organic phosphorus concentration ([DOP]) distribution across the southern Indian Ocean using observations collected on the I05 US GO-SHIP Cruise (2023) across ~33°S latitude. We quantify the longitudinal variability of [DOP] in the upper 350 m of the Indian Ocean and infer its rate of biological consumption from surface waters, contributing as an organic nutrient to sustain marine autotrophs in the region. Higher [DOP] along the eastern flank of the western gyre’s edge at 52°E (~0.085 ± 0.03 µmol/kg) compared to the gyre’s center to the west at 40°E (~0.026 ± 0.015 µmol/kg) suggests a biological consumption of ~0.06 µmol/kg within the upper 50 meters over a timescale of ~2.2 years, diagnosed from local surface drifter current velocities. The resulting autotrophic DOP consumption flux is 1.4 ± 0.05 mmol m⁻² yr⁻¹; three times higher than previous model estimates for this region. The ability of phytoplankton to utilize DOP in addition to PO₄³⁻ when inorganic nutrient supply is depleted shows resilience that could be critical for sustaining ocean ecosystems undergoing warming and the associated redistribution of ocean surface currents.
Introduction

The cores of subtropical ocean gyres, located between ~10° and 40° latitudes, tend to be oligotrophic, or low in biological productivity, due to the physical circulation limiting nutrient supply. Nutrient injection to the ocean surface is required to maintain productivity and is dominated by vertical processes over most latitudes (Letscher et al, 2016). However, subtropical gyres mostly lack vertically injected nutrients due to the largescale downwelling (sinking of surface waters) which occurs. Inorganic nitrogen and phosphorus supply typically represent the limiting factor for phytoplankton growth and organic matter export through the water column. These autotrophs preferentially consume inorganic nutrient forms because inorganic P and N molecules are small and thus easily assimilated. P and N in seawater are also found within organic molecules which are larger (ca. 10s to 1000s Daltons) and require enzymatic activity (e.g. alkaline phosphatase in the case of phosphorus esters) to be assimilated (Whitney and Lomas 2018). Phosphorus is of particular importance because its total supply to the ocean is controlled by the weathering of rocks on land playing out over geological timescales unlike nitrogen for which the marine N reservoir is replenished on annual to decadal timescales by the cyanobacteria-mediated process of nitrogen fixation (Tyrrell, 1999). As such at nearly all densities and ocean basins, phosphorus, compared to carbon and nitrogen, is preferentially remineralized nearly twofold by marine microbes (Letscher and Moore, 2015). Looking at inorganic nutrients alone would suggest oligotrophic gyres to have limited productivity (Letscher et al, 2022). However, this does not correlate with the observed net productivity in these regions, with lateral inputs and biological uptake of organic nutrients implicated as additional potential sources (Letscher et al, 2016). Up to half of the total export production from the euphotic zone globally could be represented by the subtropical gyres (Emerson et al, 1997, as
cited in Abell et al, 2000). Therefore, understanding DOP cycling is paramount for understanding the sustenance of primary productivity in oligotrophic regions, covering 60% of the world surface ocean (Abell et al, 2000).

Models of ocean circulation coupled with biological productivity within subtropical oligotrophic gyres indicate dissolved organic phosphorus (DOP) may be used in place of inorganic phosphorus (PO$_4^{3-}$) by marine autotrophs (Letscher et al, 2016; 2022). A recent model study estimates DOP contributes 14% of the required P in the global ocean for sustaining marine phytoplankton growth (Letscher et al, 2022). Direct uptake of DOP by phytoplankton influences rates of global net primary productivity (NPP) and nitrogen fixation (Letscher and Moore, 2015). An earlier model suggests including DOP as a P source to have a positive influence on NPP and N$_2$ fixation by rates of ~8% and ~33%, respectively (Letscher & Moore, 2015). The lack of analysis technology and techniques has limited our understanding of global marine DOP concentration measurements (Liang et al, 2022); DOP cannot be measured directly, so data cannot easily be gathered aboard cruises alongside other at-sea oceanographic and biogeochemical measurements. To date, field studies of these processes to test the model predictions have been focused in the Atlantic and Pacific Oceans.

To address this observational shortcoming, we obtained samples for DOP analysis from the Indian Ocean. The Indian Ocean circulation exhibits several unique patterns compared to the other ocean basins. Strong current diversions in the subtropics result in recirculation in the western and central regions of the basin, with diverging recirculations observed at 65º and 95ºE (Stramma and Lutjeharms, 1997). These recirculations impact the physical oceanography of the area, which directly impacts the DOP distribution. The recirculation around 95ºE interrupts the southern subtropical gyre, resulting in the major counterclockwise gyre located towards the
westward edge of the basin and a minor clockwise gyre located towards the eastern edge of the basin (Figure 7). Since the Coriolis effect in the southern hemisphere deflects flow towards the left, clockwise circulation results in upwelling and counterclockwise circulation results in downwelling. These physical processes impact the injection of inorganic nutrients (i.e. PO$_4^{3-}$) to surface waters. Higher PO$_4^{3-}$ stress leads to higher DOP consumption rates (Liang et al., 2022), which has been largely unstudied in the Indian Ocean. Here we investigate the DOP distribution and consumption across the Indian Ocean from the I05 US GO-SHIP Cruise (2023) across ~33ºS latitude.

This research is aimed to fill in gaps in knowledge about the phosphorus biogeochemistry in the Indian Ocean and quantify the longitudinal variability of DOP. This assessment will give insight to whether the distribution of DOP concentrations is indicative of DOP consumption by marine autotrophs as an organic nutrient. We also quantify the potential rate of autotrophic DOP consumption based on concentration gradients observed in the surface waters coupled with surface current velocities.

**Methods**

Water samples were collected in the Indian Ocean from July 22, 2023 to September 14, 2023 on the I05 US GO-SHIP Cruise aboard the *R/V Ronald H. Brown*, sailing west from Fremantle, Australia to Cape Town, South Africa (Figure 1). Briefly, seawater is gravity filtered through a 0.7 µm GF/F 47mm filter with ~40 mL collected in a glass EPA vial. The sample is acidified to pH 2 with HCl and stored refrigerated until analysis back onshore at the lab of Prof. Letscher at UNH.
Figure 1 (Blue line) I05 US GO-SHIP cruise transect collected from July 22, 2023 to September 14, 2023 spanning from Fremantle, Australia to Cape Town, South Africa. The nominal latitude is 33°S.

DOP is computed as the difference of total dissolved phosphorus (TDP) and soluble reactive phosphorus (SRP) using Equation 1:

\[ \text{DOP} = \text{TDP} - \text{SRP} \]  

Soluble reactive phosphorus is the inorganic phosphorus, or phosphate (PO$_4^{3-}$). Nutrient analysts aboard the cruise determined SRP values photometrically using acidic molybdate and antimony, known as the molybdenum blue method. The antimony phospho-molybdate complex created by the reaction between these chemicals is reduced to phosphomolybdenum blue via ascorbic acid. The concentration of SRP is then determined using Equation 2:

\[ \text{Absorbance} = (\text{Slope}) \times (\text{Concentration}) + \text{Intercept} \]

The slope and intercept are found with a calibration curve using the following known concentrations of PO$_4^{3-}$: 0.025µM, 0.05µM, 0.15µM, 0.5µM, 1.0µM, and 2.5µM. TDP measurements were made using a SEAL Analytical AQ300 Discrete Analyzer system. Samples
are first placed on a shaker table overnight to dislodge aqueous P from the interior glass walls of the storage vial and then digested prior to analysis with an oxidizing acidic (pH = 0.7) potassium persulfate reagent (POR). Digestion converts all organic phosphorus forms to \( \text{PO}_4^{3-} \). For sample volumes of 5mL, 0.4mL of POR is added. After digestion, the same colorimetric method is used via the AQ300. Deeper blues (higher absorbances) indicate higher phosphorus content. TDP values are calculated using the same absorbance equation, but are also adjusted to the POR blank using Equation 5 resulting from the following mass balance derivation:

\[
(3) \quad [\text{PO}_4^{3-}]_{\text{meas}} \cdot V_{\text{total}} = [\text{TDP}]_{\text{samp}} \cdot V_{\text{samp}} + [\text{PO}_4^{3-}]_{\text{POR}} \cdot V_{\text{POR}}
\]

\[
(4) \quad [\text{TDP}]_{\text{samp}} = ([\text{PO}_4^{3-}]_{\text{meas}} \cdot V_{\text{total}} - [\text{PO}_4^{3-}]_{\text{POR}} \cdot V_{\text{POR}}) / V_{\text{samp}}
\]

\[
(5) \quad TDP_{\text{samp}} = ([\text{PO}_4^{3-}]_{\text{meas}} \cdot 5.4 \text{ mL} - [\text{PO}_4^{3-}]_{\text{POR}} \cdot 0.4 \text{ mL}) / 5 \text{ mL}
\]

Samples were analyzed in triplicate and were computed and averaged using Microsoft Excel. Figures were generated using Ocean Data View (ODV). The uncertainty on DOP concentration determinations is ~5-10% or 0.002 to 0.02 µmol/kg, computed from the combined reproducibility variances of the measured TDP and SRP concentrations added in quadrature.

**Results**

The DOP distribution in the subtropical Indian Ocean varies both longitudinally and with depth (Figure 2). Surface concentrations (≤50 m) within the western subtropical gyre’s center at ~40ºE are ~ 0.026 ± 0.015 µmol/kg. Concentrations at the gyre’s eastern edge at ~52ºE increase to ~ 0.085 ± 0.03 µmol/kg. Moving eastward, surface DOP concentrations then decrease to ~ 0.048 ± 0.033 µmol/kg between 60ºE–90ºE and increase to ~ 0.062 ± 0.030 µmol/kg between 90ºE–100ºE. Higher concentrations at depth, ~ 0.12 µmol/kg, are found within 100-350 m from 55ºE – 90ºE. Potential density anomalies (\( \sigma_0 \)) feeding this region fall between 26.2 and 26.6 kg/m³ with surface outcrops in the eastern gyre near 90º to 105ºE (Figure 2).
Figure 2 [DOP] in µmol/kg interpolated over 350 m depth at ~33ºS in the Indian Ocean from ~30ºE – 105ºE. Green indicates higher concentrations (~0.12 µmol/kg), whereas blue/purple indicates lowest concentrations (~0.05 µmol/kg to undetectable). Smooth black lines indicate relevant potential density anomalies in $\sigma_0$ [kg/m³] (i.e., isopycnals).

Figure 3 [$PO_4^{3-}$] (PHSPHT) in µmol/kg interpolated over 350 m depth at ~33ºS in the Indian Ocean from ~30ºE – 105ºE. Red indicates highest concentrations (>0.6 µmol/kg), whereas deep blue/purple indicates lowest concentrations (~0.1 µmol/kg).

Phosphate concentrations are low (<0.2 µmol/kg) in the upper 100 m other than a section of higher concentrations (~0.35 µmol/kg) at ~95ºE longitude (Figure 3). [$PO_4^{3-}$] increase with depth with a water mass of higher concentrations from 200-350m depth between ~60–80ºE and another between ~85ºE–110ºE (Figure 3).
DOP makes up a higher percentage of TDP in the upper 200 m compared to deeper waters (Figure 4). In general, DOP makes up less than half of the TDP in the water column, with the remaining content being SRP. Waters of 30-40% DOP are mostly confined to the upper 150 m, with peak values between 40-60% in the upper 25 m at ~47ºE, 55ºE, 75ºE, and 100ºE (Figure 4).
Figure 5 Average [DOP] and [PO$_4^{3-}$] in the upper 50m of the Indian Ocean at ~33ºS from ~30ºE – 105ºE. Blue circles indicate [DOP]; orange circles indicate [SRP], or [PO$_4^{3-}$]. Low [PO$_4^{3-}$] is considered to be ~0.01-0.3 µmol/kg (Letscher et al, 2022).

Longitudinal variability of [DOP] and [PO$_4^{3-}$] in the upper 50 m (Figure 5) follow a roughly similar fluctuation pattern other than in peak regions, discussed later. In general, PO$_4^{3-}$ concentrations are low (mostly <0.3 µmol/kg) in the upper 50 m, with a peak of 0.39 ± 0.02 µmol/kg at 99ºE. [DOP] oscillates longitudinally with peaks observed at roughly 40, 55, 75, and 93ºE and troughs at roughly 45, 65, 85, and 105ºE. [DOP] peaks loosely correspond with peaks of [PO$_4^{3-}$], and [DOP] troughs with troughs of [PO$_4^{3-}$].

Discussion

The longitudinal gradients of DOP within the upper 50-100 m (the euphotic zone) can give insight to its potential for photosynthetic utilization by marine autotrophs. Here we observe elevated DOP concentrations within the upper 50 m at the western gyre’s eastern edge at ~52ºE (~0.085 ± 0.03 µmol/kg) compared to the western gyre’s center around 40ºE (~0.026 ± 0.015 µmol/kg) (Figure 6). Given the counterclockwise flow of the western gyre (Fig. 7), Ekman transport should be to the west near 33ºS 52ºE, leading to surface convergence near the gyre center at ~40ºE. We interpret this gradient to arise from autotrophic consumption of DOP given its depth in the water column and the fact that no gradient in [DOP] would be expected if it behaved as a passive tracer within the prevailing surface current flow, which is not observed.
Figure 6 Interpolated [DOP] in the upper 100 meters in the Indian Ocean at ~33ºS. The red star indicates an area of higher concentration at the eastern edge of the western gyre; the yellow star indicates a region of lower concentration in the gyre's center. The arrow indicates the direction of net zonal flow of surface waters.

Figure 7 Indian Ocean circulation based off sea surface height measurements in 1992 courtesy of Stramma and Lutjeharms (1997). Stars correspond with those in Figure 6.

The rate of autotrophic consumption can be quantified using Equation 6:

\[
DOP_{\text{cons}} = \frac{(\Delta DOP)(D_{\text{Ek}})}{T_{52^\circ-40^\circ E}}
\]

\(DOP_{\text{cons}} = 1.4 \pm 1.8 \text{ mmol m}^{-2} \text{ yr}^{-1}\), where the mean [DOP] gradient (\(\Delta DOP\)) = 0.06 mmol m\(^{-3}\) is integrated over the depth of the Ekman layer (\(D_{\text{Ek}}\)) = 50 m. Uncertainty on the \(DOP_{\text{cons}}\) value
represents the combined uncertainty from the analytical variability in the DOP concentrations, and the variability around the mean concentrations of DOP measured in situ as well as the current velocity. High uncertainty most strongly reflects the variable surface velocities which varied by ±129%. The timescale of surface current flow to transit the 12 degrees of longitude westward at ~33°S \((T_{52°-40°E})\) is \(≈ 2.2\) yr, computed from the east to west (zonal) velocity, \~1.64 cm/s, extracted from a climatology of surface current drifters (Laurindo et al, 2017)\(^7\). This autotrophic consumption estimate is an upper bound since we assume only westward flow; meridional and vertical flow vectors could influence the distribution alongside biological uptake. A previous model study estimated autotrophic DOP uptake in this region to be \(0.49 \pm 0.07\) mmol m\(^{-2}\) yr\(^{-1}\) (Letscher et al, 2022)\(^10\); our estimate is almost 3 times higher. Letscher et al (2022)\(^10\) also predicted the fraction of the biological pump supported by DOP to be \~14% in this region; our higher value indicate DOP could be more important in sustaining autotrophic P demand across the subtropical Indian Ocean. A previous study suggests enhanced autotrophic consumption of DOP when [PO\(_4^{3-}\)] \(\leq 0.2\) µmol/kg (Letscher et al, 2022)\(^10\), which corresponds with the conditions in this study region.

Overall, net community production (NCP) in ocean subtropical gyres tends to be supported by the resulting gradient from elevated DOP production along the outer gyre regions and depressed concentrations within the gyre (Letscher et al, 2022)\(^10\). The circulation patterns in the Indian Ocean are not as consistent as other ocean basins, making the longitudinal distribution more variable. The subtropical gyre is also offset towards the westward region of the ocean basin closer to the tip of South Africa, which influences the inconsistency resulting from diverging currents and recirculation patterns towards the eastward boundary observed in Figure 7. Generally, [DOP] tends to be higher near and along the surface flow of circulating currents and
lower in between (i.e. the western and eastern gyres). Recirculation at ~95°E (Stramma and Lutjeharms, 1997) could explain the higher nutrient concentrations (PO$_4^{3-}$) within the surface-directed flow in this area (Figure 2). Recirculation in this region is clockwise (Figure 6b), resulting in upwelling. The isopycnals defined in Figure 2 demonstrate this flow pattern. Upwelling brings inorganic nutrient-rich waters from below towards the surface. This injection of phosphate is preferentially consumed over DOP by marine autotrophs. Unused reserves of DOP and newly formed inputs resulting from primary production are subsequently subducted and flow westward down the 26.2 and 26.4 kg/m$^3$ isopycnals (Figure 2). This could help explain why [DOP] in the upper 50 m is not elevated with the elevated [PO$_4^{3-}$] in this region (Figure 5); the water containing these reserves carries it away downwards and westward. Other regions of elevated [DOP] in the upper 50 m correspond with elevated [PO$_4^{3-}$] (e.g. 39, 54, 59, and 71°E) (Figure 5) likely because DOP is a product of primary productivity, so slightly higher [PO$_4^{3-}$] leads to both reduced DOP consumption and enhanced DOP production. This relationship also explains the distribution of the ratio of DOP:TDP presented in Fig. 4, with higher percentages corresponding to areas with slightly elevated [PO$_4^{3-}$] relative to the neighboring areas.

Other advective influences could explain the water mass of higher [DOP], ~0.12 µmol/kg, between the 26.5 and 26.6 kg/m$^3$ isopycnals (Figure 2). Koch-Larrouy et al (2010) classify three sites for subantarctic mode water (SAMW) ventilation in the Indian Ocean based on the density signatures of the water masses: light SAMW (26.5-26.7 kg/m$^3$), denser SAMW (>26.7 kg/m$^3$), and deep/densest SAMW (26.8 – 26.85 kg/m$^3$). The light SAMW ventilates between 50 and 70°E upstream of the Kerguelen plateau (~55°S) and subducts into the western gyre (Koch-Larrouy et al, 2010). The origin of this mass of SAMW is the Agulhas retroflection, located south of the southern tip of South Africa (Koch-Larrouy et al, 2010). The dense SAMW forms south of the
Agulhas retroflection, and the deep/densest SAMW originates in Leeuwin Current waters, Taman Sea (Pacific) waters, and surface waters of the Antarctic (Koch-Larrouy et al, 2010). We hypothesize the elevated DOP distribution observed between 55-90°E to be a result of northeastward advection and subsequent ventilation of the lightest branch of SAMW from its formation region. DOP observations from the SAMW light branch formation region do not exist to confirm if SAMW subducts with elevated concentrations of DOP produced in surface waters. However, elevated concentrations of relatively fresh marine DOC are known to occur in other mode water formation regions globally such as the eighteen degree mode water of the North Atlantic (Hansell and Carlson, 2001).

SAMW in the Indian Ocean is warmer and lower in O₂ (271 ± 8.2 vs. 292 ± 6.2 µmol/kg), [NO₃⁻] (13.3 ± 2.9 vs. 21.5 ± 1.2 µmol/kg) and [DIC] (2120 ± 6.3 vs. 2135.1 ± 7.5 µmol/kg) compared to the Pacific Ocean (Bushinsky and Cerovečki, 2023). Biogeochemical changes in SAMW are difficult to track but are important because this water mass is one of the main channels for nutrient addition to other ocean basins (Álvarez et al, 2011). Phosphate concentrations decreased (−0.09 ± 0.01 µmol/kg) in the western Indian Ocean sector of SAMW from 1987 to 2002 (Álvarez et al, 2011). Both anthropogenically and naturally induced changes to ocean systems have foreshadowed a reduced circulation in the subtropical Indian Ocean gyre, as indicated by reduced inorganic carbon storage within SAMW (Álvarez et al, 2011). This further exemplifies the importance of monitoring biogeochemical fluxes in the Indian Ocean and having a comprehensive understanding of how these fluctuations will impact ocean ecosystems.

**Conclusion**

We found the subtropical Indian Ocean at the nominal latitude of ~33°S to have variable surface gradients of [DOP] on the order of 0.05 to 0.15 µmol/kg (Figure 2, 5). The surface
gradient from the eastern edge of the western subtropical gyre toward the gyre’s center was found to have an autotrophic DOP consumption rate of $1.4 \pm 0.05 \text{ mmol m}^{-2} \text{ yr}^{-1}$ when only westward flow is taken into consideration, which is a value almost three times higher than previous model estimates. In addition, a water mass of elevated [DOP] on the order of 0.12 $\mu$mol/kg was observed below 200 m near the central southern Indian Ocean, likely attributable to SAMW.

Liang et al (2022) investigated the roll of iron stress in the distribution, production, and consumption of DOP in ocean basins such as the Atlantic and Pacific. They use non-photochemical quenching (NPQ) corrected remotely sensed fluorescence quantum yield ($\phi_{\text{sat}}$) from the MODIS-Aqua ocean color satellite as a proxy for iron stress, with higher values representing higher iron stress (Liang et al, 2022). They found NPQ-corrected $\phi_{\text{sat}}$ and DOP stocks in the upper 50m of upwelled regions of the Pacific Ocean basin to have a strong negative correlation, meaning alleviated iron stress leads to more DOP production (Liang et al, 2022). Iron stress can impact the success of alkaline phosphatase (a necessary enzyme for DOP consumption by phytoplankton), which can lead to higher DOP stocks due to the inability of autotrophs to utilize it as an alternative P source (Liang et al, 2022). Estimates of $\phi_{\text{sat}}$ from Behrenfeld et al (2009) indicate the subtropical Indian Ocean at ~33°S to have a low $\phi_{\text{sat}}$ (~1-2%), which would place this region in the lower two quadrants (indicating alleviated iron stress) of Figure 3 of the Liang et al (2022) analysis on the correlation between PO$_4^{3-}$ stress, iron stress, and DOP accumulation. Since PO$_4^{3-}$ stress is enhanced in the western basin and alleviated in regions of the eastern basin (Figure 3), the Indian Ocean would be expected to experience significant net DOP loss in the western regions (like the western South Pacific, western North Pacific, and North Atlantic) and significant DOP accumulation in the eastern basin (like the
eastern South Pacific, eastern North Pacific, and West Florida Shelf) according to Liang et al (2022)\textsuperscript{11}. In other words, when iron is available and PO$_4^{3-}$ stress is enhanced, phytoplankton are more likely/able to use DOP as an alternative P source, as observed in the Pacific and Atlantic Ocean basins (Liang et al, 2022)\textsuperscript{11} and now here for the western Indian Ocean. Further research should more accurately quantify this correlation in the Indian Ocean by specifically focusing on iron availability and its relationship to DOP accumulation with direct observations within this basin.

Estimating autotrophic DOP consumption rates with field observations of DOP gradients across ocean basins is important for gauging phytoplankton resilience to climate change. As the ocean changes with the climate and nutrient availability becomes more unpredictable, the fate of phytoplankton might be more optimistic than previously assumed since DOP concentrations are comparable to PO$_4^{3-}$ in many ocean regions including the southern Indian Ocean studied here. Warmer oceans are more stratified, which limits the vertical mixing necessary for supplying inorganic nutrients to the surface waters from depth. The ability of phytoplankton to utilize DOP in place of PO$_4^{3-}$ shows a resilience that could be critical for sustaining ocean ecosystems. Further research should evaluate species-specific DOP consumption rates in response to phosphate and iron stress. More detailed analysis without the assumption of only westward flow would generate a more representative DOP consumption rate for this subtropical gyre. Analysis of DOP supply and consumption in the northern Indian Ocean would provide a more comprehensive overview of this understudied ocean basin including the large seasonal impacts of monsoons in this region.
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