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Production and respiration rates in the Arabian Sea during the 1995 Northeast and Southwest Monsoons

Mary-Lynn Dickson[a,*], Joseph Orchardo[a], Richard T. Barber[b], John Marra[c], James J. McCarthy[d], Raymond N. Sambrotto[c]

[a]*Graduate School of Oceanography, University of Rhode Island, Narragansett, RI 02882, USA*
[b]*Nicholas School of the Environment, Duke University, Beaufort, NC 28156, USA*
[c]*Marine Biology, Lamont-Doherty Earth Observatory, Columbia University, Palisades, NY 10964, USA*
[d]*Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138, USA*

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Abstract

In this paper we examine the relationships among oxygen, carbon and nitrogen production and respiration rate measurements made in the Arabian Sea during the 1995 Northeast (NEM) and Southwest (SWM) Monsoons. Increased biological production characterized the SWM, with rates 12–53% higher than the NEM. In most cases, we found remarkable similarity in production rates during the two monsoons and an absence of strong spatial gradients in production between nearshore and offshore waters, especially during the SWM. Daily ^{14}C and total ^{15}N production underestimated gross C production, and at the majority of stations ^{14}C and total ^{15}N production were either the same as net C production or between gross and net C production. Moreover, new production ($^{15}NO_3$), scaled to carbon, was substantially less than net C production. Approximately 50% of the $PO^{14}C$ was metabolized during the photoperiod, with smaller losses (7–11%) overnight. The simplest explanation for the discrepancy between gross and total ^{15}N production and between net C and new production was the loss of ^{15}N-labeled particulate matter as dissolved organic matter. Partitioning of metabolized gross C production into respiratory and dissolved pools showed distinct onshore–offshore distributions that appeared to be related to the composition of the phytoplankton assemblage and probably reflected the trophodynamics of the ecosystem. The percentage of gross C production released as dissolved organic carbon (DOC) was highest in the nearshore waters where diatoms dominated the phytoplankton assemblage, while community respiration was a more important fate for production further offshore where picoplankton prevailed. In general, stations that retained more gross C production as net production (i.e., high net C/gross C ratios) had higher rates of DOC production relative to community respiration. Locations where community respiration exceeded DOC production were characterized by low rates of net C production and had low net C/gross C ratios. In those ecosystems, less net C production was retained because higher metabolic losses reduced gross C production to a greater extent than at the more productive sites.

* Corresponding author. Fax: + 1-401-874-6811.
E-mail address: dickson@gso.uri.edu (M.-L. Dickson).

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1. Introduction

The Arabian Sea is a unique ecosystem that undergoes seasonal oscillations in primary production in response to atmospheric monsoonal forcing. Like other oceanic regions that experience monsoons, it is characterized by strong seasonal variations in wind direction involving the complete reversal of the wind field (Tomczak and Godfrey, 1994). During a monsoon, energy is transferred from the atmosphere to the ocean, affecting mixed-layer development and the nutrient supply to the euphotic zone. As a result, the distribution of nutrients and primary production varies areally and seasonally within the basin, from extremely eutrophic coastal environments to oligotrophic conditions offshore. Unlike temperate and high latitude ecosystems where temporal variability in primary production is the result of seasonal variation in solar radiation, in the Arabian Sea variability is linked to the monsoonal circulation under conditions of relatively constant solar radiation (Smith et al., 1991).

Two monsoons dominate atmospheric and oceanic processes in this region. The Northeast Monsoon (NEM) typically takes place from November to February while the Southwest Monsoon (SWM) occurs from June to September (Wyrtki, 1973; Weller et al., 1998). Climatic variations in the northern Arabian Sea originate from different thermal responses of the Indian Ocean and Tibetan Plateau to seasonal variations in insolation. In winter (NEM), the entrainment of water from depth occurs over much of the basin due to cooling of the sea surface from winds that originate over the Tibetan plateau. The SWM is the stronger of the two monsoons, being characterized by higher wind speeds, deeper mixed-layer depths, and the accumulation of more phytoplankton biomass (Bauer et al., 1991). In summer (SWM), vertical mixing and Ekman dynamics induce coastal and open ocean upwelling in the region of positive wind stress curl north of the Findlater Jet (the axis of the strongest southwest winds). South of the jet, where the wind stress curl is negative, convergent flow deepens the mixed-layer entraining nutrients into the euphotic zone (McCreary and Kundu, 1989; Brock et al., 1991; Brock and McClain, 1992). In 1995 the NEM was distinguished by steady but moderate winds, clear skies, relatively dry air and a net heat loss from the surface ocean while, in contrast, the SWM had strong winds, cloudy skies, moist air, and a net oceanic heat gain (Weller et al., 1998). Furthermore, when meteorological and oceanographic time-series data collected during the US JGOFS study were compared to recent climatologies, it was found that 1994–95 was a typical year in the northwestern Indian Ocean.

The biological response to monsoonal forcing is dramatically illustrated in sediment-trap data (Nair et al., 1989) and ocean color images (Yoder et al., 1993). Nutrient inputs from depth and stratification of the mixed layer favor the accumulation of large amounts of phytoplankton biomass in the euphotic zone. The annual production cycle is dominated by high rates of primary production during the winter (NEM) and summer (SWM), which are interspersed between periods of low production associated with the intermonsoon seasons (Smith, 1984). Previous studies found that primary production exceeded $1.7\,\mathrm{g\,C\,m^{-2}\,d^{-1}}$ during the SWM compared to 0.3 and $< 0.1\,\mathrm{gC\,m^{-2}\,d^{-1}}$ for the NEM and intermonsoon seasons (Brock et al., 1994). Other studies in the region have reported a high degree of spatial (Krey, 1973; Krey and Babenerd, 1976; Owens et al., 1993) and temporal (Robinson and Williams, 1999) variability in production rates. Annual production in the basin, estimated with remotely sensed data, varies by a factor of three, from ~ 450 gC $\mathrm{m^{-2}}$ next to the coast and extending seaward, to $< 150\,\mathrm{gC\,m^{-2}}$ in offshore waters (Behrenfeld and Falkowski, 1997). However, unlike previous studies, our results show remarkable

similarity in production rates during the winter (NEM) and summer (SWM) and the presence of weak spatial gradients in integrated production between nearshore and offshore waters, especially during the SWM.

The objective of this work in the overall context of the US JGOFS Arabian Sea Process Study was to investigate the biological response to monsoonal forcing, and improve our understanding of the role that biological processes play in determining the carbon flux. In this paper we report gross and net C production rates derived from oxygen measurements and compare them with ^{14}C and ^{15}N production rates made during the 1995 NEM and SWM. We assess seasonal and spatial patterns in the various integrated production rates and evaluate them against macronutrient distributions, phytoplankton growth rates (Caron and Dennett, 1999; Landry et al., 1998) and the phytoplankton species composition (Garrison et al., 1998; Campbell et al., 1999; Dennett et al., 1999). We examine assimilation numbers, based on gross O_2 production measurements, to address nutrient sufficiency of the phytoplankton and to alert us to potential bottle effects compromising the rate data. Finally, we estimate the partitioning of metabolized gross production into respiratory losses and DOC production and discuss the implications of these results.

2. Methods

Production rate measurements were made during two cruises in the Arabian Sea on the R/V *Thomas G. Thompson*. The NEM cruise (TN043) took place from January 8 to February 4, 1995, while the SWM cruise (TN049) occurred between July 17 and August 15, 1995. Data collected on these cruises are available from the US JGOFS Data Management Office (http://usjgofs.whoi.edu).

2.1. Sampling protocol and cruise track

The cruise track for the US JGOFS Arabian Sea Process Study covered the area between 10°00'N and 22°23'N, from 56°45'E to 68°45'E (Fig. 1). Twenty-seven stations were occupied along two transects, hereafter referred to as the N (north) and S (south) lines. Eleven stations located on the northern leg were occupied first, beginning with station N1 closest to the Omani coast and finishing with station N11. This was followed by a single station, M1, situated between the N- and S-lines. The S-line consisted of 15 stations from S15 (farthest offshore) to S1 (next to the coast). Six stations designated as "long stations" (N7, S15, S11, S7, S4 and S2) were occupied for 48 h. Production measurements were made at these stations by incubating samples in situ and/or in deck incubators cooled with running surface seawater. At the "intermediate stations" (N2, N4, N6, N9, N11, S13, S9, S3, S1) samples for production and community respiration rates were collected when the ship arrived on station, just prior to sunrise whenever possible, and all incubations were carried out in shipboard incubators.

Seawater samples for the productivity experiments were collected using 30-l Go-Flo bottles attached to a trace metal-clean rosette (Hunter et al., 1996). During the second half of the SWM cruise, samples were collected using 10-l Niskin bottles attached to an epoxy-coated rosette frame that housed a Seabird CTD. Measures and Vink (1999) compared the iron concentration in seawater samples collected with both systems and found no systematic difference between them.

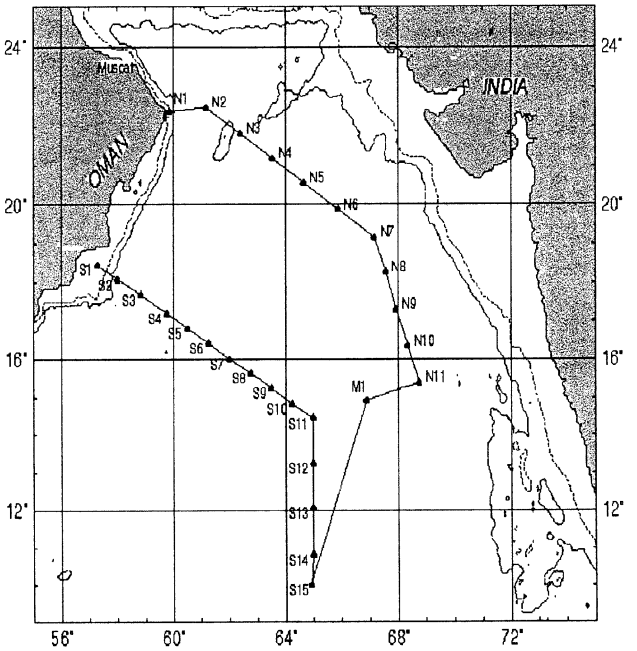

Fig. 1. Map of station locations during the 1995 US JGOFS Arabian Sea Process Study. The track consisted of a northern (N) and southern (S) line of stations that were occupied in a clockwise direction beginning with N1 and concluding with S1.

Samples for the oxygen productivity experiments were collected from six depths corresponding to 85, 44, 27, 15, 7, and 4% of surface irradiance (E_o). Unlike the ^{14}C and ^{15}N measurements, oxygen production and respiration rate measurements did not include samples from 1 and 0.1% E_o due to extremely low oxygen concentrations at those depths. In this paper, rate data from the 1 and 0.1% E_o have been excluded from the analysis and all integrations were calculated to the 4% E_o. Twenty-four hour ^{14}C production below the 4% E_o and down to the 1% E_o was $12 \pm 2\%$ (NEM) and $7 \pm 2\%$ (SWM) of water column production.

Care was taken to minimize contamination of the collected seawater during sampling by using trace metal free powderless PVC gloves and silicon tubing that was cleaned prior to sampling by rinsing several times with 10% HCl, followed by several rinses with distilled/deionized water. Quartz incubation bottles having a nominal volume of 100 ml were used for the oxygen production and respiration measurements. The bottles were filled and allowed to overflow three to five volumes of seawater before being closed with a glass stopper. Protocols for the ^{14}C measurements are given in Barber et al. (2001), while the ^{15}N methodologies are reported by McCarthy et al. (1999) and Sambrotto (2001). During the NEM, nitrogen assimilation measurements were made with ^{15}N-labeled NO_3^-, NO_2^-, and NH_4^+, while during the SWM the substrates used were NO_3^-, NH_4^+ and urea. NH_4^+ and urea uptake rates have been corrected for isotope dilution.

At the long stations, the primary productivity array was launched before sunrise and recovered within an hour after sunset. Once recovery of the array was completed, productivity samples were

either processed immediately or placed in shipboard incubators overnight and processed the following morning when 24 h of incubation time had elapsed. Gross and net O_2 production and respiration samples were incubated for 24 h and ^{14}C samples were incubated for 12 (i.e., the duration of the photoperiod) and 24 h. Labeled nitrogen samples were incubated in deck incubators for 4–6 h (McCarthy et al., 1999; Sambrotto, 2001). During the NEM, uptake experiments were begun at 0600, 1200 and 2200 h (McCarthy et al., 1999). Daily nitrogen uptake rates were calculated by summing the uptake for both halves of the solar day and at night. Total ^{15}N production was determined by summing the daily uptake rate for each substrate.

Seawater temperatures were monitored in the 85 and 4% E_o ^{14}C deck incubators and the in situ array during the SWM with waterproof Optic StowAway temperature loggers (Onset Computer Corp., Pocasset, MA). Resolution of the loggers is 0.15°C. The temperature difference between the ^{14}C incubators and in situ array at each irradiance level was computed throughout the photoperiod using 450 pairs of measurements. Seawater temperatures recorded in the in situ array increased by about 0.5°C over the photoperiod. At stations S2, S11 and S15 seawater temperatures in the 85% E_o incubators were 0.9 ± 0.4 to 1.8 ± 0.9°C (mean $\pm$ SD) higher than in situ, while in the 4% E_o incubator, water temperatures were 0.4 ± 0.2 to 0.6 ± 0.2°C warmer. The largest degree of warming was observed at station N7 where water temperatures were 3.0 ± 1.6 and 3.7 ± 0.2°C higher in the 85 and 4% E_o incubators, respectively, than in situ. Overnight temperatures in the incubators were maintained to within 0.5°C of the ambient sea surface temperature.

2.2. Production and respiration measurements

Gross O_2 production is determined by spiking seawater samples with ^{18}O-labeled water and measuring the amount of ^{18}O-labeled O_2 that is produced photosynthetically via the Hill reaction (Bender et al., 1987; Grande et al., 1989b). This method measures gross *primary* production. Net O_2 production is measured from changes in the $[O_2]$ in incubated bottles. This represents net *community* production and is equivalent to gross O_2 production minus the oxygen consumed by autotrophic and heterotrophic respiration.

Gross O_2 production measurements involved collecting 4 samples from each depth. Two samples per depth were extracted within an hour of collection for the initial $\delta^{18}O$ of dissolved O_2, and 2 samples per depth were spiked with 100 µl of 97 atom% enriched ^{18}O-labeled water (Cambridge Isotope Laboratories, Andover, MA) and incubated for 24 h (Bender et al., 1987). Gases were extracted from each sample using the procedure of Emerson et al. (1991). This involved transferring about 50 ml of seawater into a pre-evacuated 150 ml glass flask into which 200 µl of a saturated $HgCl_2$ solution had been dried. The pre-evacuated flasks were sealed with a glass barrel fitted with Viton O-rings. To lessen the chance of admitting air into a flask when transferring a sample, we flushed the sample port on each flask with CO_2. Back in the lab most of the water, except for 1–2 ml, was removed and the CO_2 and residual water were frozen with liquid nitrogen. The N_2, O_2 and Ar were then quantitatively collected in a stainless steel tube immersed in liquid helium. Once a transfer was completed, the sample tube was allowed to warm to room temperature. Samples were admitted into the inlet of a Finnigan MAT 252 mass spectrometer and analyzed against a standard gas mixture having an N_2, O_2 and Ar composition similar to saturated seawater (Emerson et al., 1991). We measured the $\delta^{15}N$ of N_2 and $\delta^{18}O$ of O_2 by simultaneous double collection and $\delta(O_2/Ar)$ by peak jumping with sample/reference switching (Sowers et al., 1989).

Precision ($\pm$ standard deviation) for replicate samples was better than $\pm 0.05\%$ for $\delta^{15}N$, $\pm 0.07\%$ for $\delta^{18}O$, and $\pm 2‰$ for $\delta(O_2/Ar)$.

Daily gross O_2 production was calculated from the isotopic composition of the dissolved O_2 in initial and incubated samples using the formula:

$$^{18}\text{O gross } O_2 \text{ production} = \left[\frac{\delta^{18}O(O_2)_f - \delta^{18}O(O_2)_i}{\delta^{18}O_{water} - \delta^{18}O(O_2)_i}\right] \times [O_2]_i,$$

where, the subscripts i and f refer to the isotopic composition of O_2 in initial and final samples, $\delta^{18}O_{water}$ is the isotopic composition of the water spike (and the photosynthetically produced O_2), and $[O_2]_i$ is the oxygen concentration of the initial water sample drawn from a Go-Flo or Niskin bottle.

Net O_2 production was measured from the change in the $[O_2]$ in the incubated bottles (i.e., $[O_2]_{final}$ minus $[O_2]_{initial}$). Quadruplicate initial samples were fixed with Winkler reagents (Carritt and Carpenter, 1966) after being drawn from a Go-Flo or Niskin bottle, and quadruplicate samples were incubated for 24 h in situ in the same manner as previously described for the gross O_2 samples. Initial and incubated samples were titrated together once the final samples reached thermal equilibrium, approximately 6 h after being fixed. Titrations were performed with a high precision, automated titrator configured with a 5 ml autoburette and controlled by a titration manager (Radiometer America, Westlake, OH). Analytical precision, expressed as standard deviations, was 0.04% for iodate standards and 0.07% for replicate samples.

Dark respiration rates were measured at the intermediate stations during the SWM by incubating quadruplicate samples from each depth in the dark for 24 h in shipboard incubators. Daily respiration rates were calculated as the difference between 24 h gross and net O_2 production rates (Grande et al., 1989a) and are valuable measures of respiratory activity in the water column because, unlike dark respiration rates, they include respiration in the light during the photoperiod. Daily and dark respiration rates are reported as negative fluxes, but dark respiration/net production ratios are given as positive values.

Gross and net O_2 production rates were converted to gross carbon and net carbon production rates using the equations:

$$\text{Net C production} = (\text{Net } O_2 \text{ production}/1.4),$$

$$\text{Gross C production} = [\text{Net C production} + (\text{Gross } O_2 \text{ production} - \text{Net } O_2 \text{ production})/1.1].$$

These relationships imply that net community production and new production are equivalent and gross production is the sum of new and regenerated production, also known as total production (Dugdale and Goering, 1967; Williams, 1993a). A photosynthetic quotient ($PQ = \Delta[O_2]/\Delta[CO_2]$) of 1.4, based on nitrate assimilation, was used to convert net O_2 production rates to net C rates. A PQ of 1.1 represents utilization of regenerated forms of nitrogen, primarily ammonium and urea. Photosynthetic quotients are not perfectly known; however, the values we have adopted are fairly well constrained on the basis of the biochemical composition of phytoplankton (Laws, 1991), direct measurements (Williams and Robertson, 1991), and modeling studies (Williams, 1993b). A C/N ratio of 6.6 was used to convert total ^{15}N and $^{15}NO_3$ production rates to carbon production (Redfield et al., 1963).

To estimate the amount of "new" production in the quartz bottles and to compare those values to net O_2 production rates, we measured the change in the $[NO_3^-]$ (i.e., $\Delta[NO_3^-]$) in samples incubated for 24 h. Initial $[NO_3^-]$ samples were drawn directly from the Go-Flo or Niskin bottles. At the long stations two samples per depth were incubated in situ, in parallel with samples for gross and net O_2 production. Initial and final samples were analyzed for $[NO_2^-]$ and $[NO_2^- + NO_3^-]$ with a Technicon II AutoAnalyzer following US JGOFS protocols (SCOR, 1996; Morrison et al., 1998).

The amount of gross C production respired as CO_2 and released as DOC was estimated by comparing integrated gross C, net C, $^{15}NO_3$ and total ^{15}N production rates. This involved first calculating the total amount of gross C production lost due to respiration (autotrophic and heterotrophic) and DOC production by taking the difference between integrated gross and net C production. We refer to this as "metabolized gross C production". Since gross C production and total ^{15}N production (scaled to carbon) should be equivalent, gross DOC production was estimated by subtracting integrated gross C production from total ^{15}N production (scaled to carbon). Finally, the amount of production respired by the microbial community (i.e., autotrophs and heterotrophs) was calculated as the difference between the amount of metabolized gross C production (first calculation) and gross DOC production (second calculation). Net DOC production was estimated as the difference between net C and $^{15}NO_3$ (scaled to carbon) production rates.

A model II linear regression analysis was applied to the in vitro data in order to account for measurement errors associated with the dependent and independent variables (Sokal and Rohlf, 1981). Average values are reported $\pm$ 1 standard error (SE), unless otherwise noted.

3. Results

3.1. Environmental conditions

During the NEM, cool surface water (24.5°C) was present next to the Omani coast on both the N- and S-lines, with the warmest water (27°C) found at the southernmost stations (Fig. 2a). Colder water ($\sim$ 20.5° to 24°C) was restricted to the coast during the SWM with sea surface temperatures (SSTs) away from the coast typically between 26 and 28.5°C (Fig. 2a). Most stations were 0.5 to 4°C warmer during the SWM compared to the NEM. The greatest degree of warming occurred at stations N2 to N8 where SSTs increased by 3–4°C, while temperatures on the S-line only increased by 1–2°C. Only stations nearest the coast (S1, S2, N1) and station S6 were warmer during the NEM. Mixed-layer depths (MLD) were 18 to 54 m deeper during the NEM and in both seasons the MLD exceeded the depth of the 4% E_o (Table 1). With the exception of stations S7 and S11, the 4% E_o was deeper during the NEM than the SWM.

The NEM was characterized by surface waters with $[NO_3^-]$ between $\sim$ 1 and 4.5 μM, except at stations S3, S14 and S15 where the $[NO_3^-]$ was between 0.1–0.5 μM (Fig. 2b). A higher degree of mesoscale variability was apparent in the nutrient field during the SWM (Fig. 2b). At this time, NO_3-rich waters (i.e., $\geqslant$ 5 μM) were found next to the coast on the N-line, but extended further offshore on the S-line due to the presence of an eddy or filament that originated in high nutrient, nearshore waters (Morrison et al., 1998; Latasa and Bidigare, 1998). Particularly notable were the

low $[NO_3^-]$, on the order of 0.1 μM, at the majority of stations away from the coast. This situation was unexpected as it was initially thought, based on a climatology of mixed-layer depths (Molinari et al., 1986; Rao et al., 1989), that waters north of the Findlater Jet would have elevated nutrient concentrations throughout the SWM.

Dissolved $[O_2]$ were between 4–5 $ml\,l^{-1}$ down to the 4% E_o and decreased rapidly to approximately 0.1 $ml\,l^{-1}$ at the 1% E_o (data not shown). During the NEM, surface waters were mostly undersaturated in O_2, with the exception of stations S1–S4, which were oversaturated by 2–6% (Fig. 2c). In these waters, high chlorophyll *a* concentrations (2–3 $\mu g\,l^{-1}$) and O_2 production rates were measured, suggesting that biological production was responsible for the supersaturation. During the SWM, surface waters next to the coast were highly undersaturated (75–86%) with respect to O_2. Stations away from the coast on the N-line also tended to be slightly undersaturated but supersaturated along the S-line. The highly undersaturated nearshore waters, coupled with high $[NO_3^-]$ (Fig. 2b), indicate upwelling was occurring at the coastal stations during the SWM.

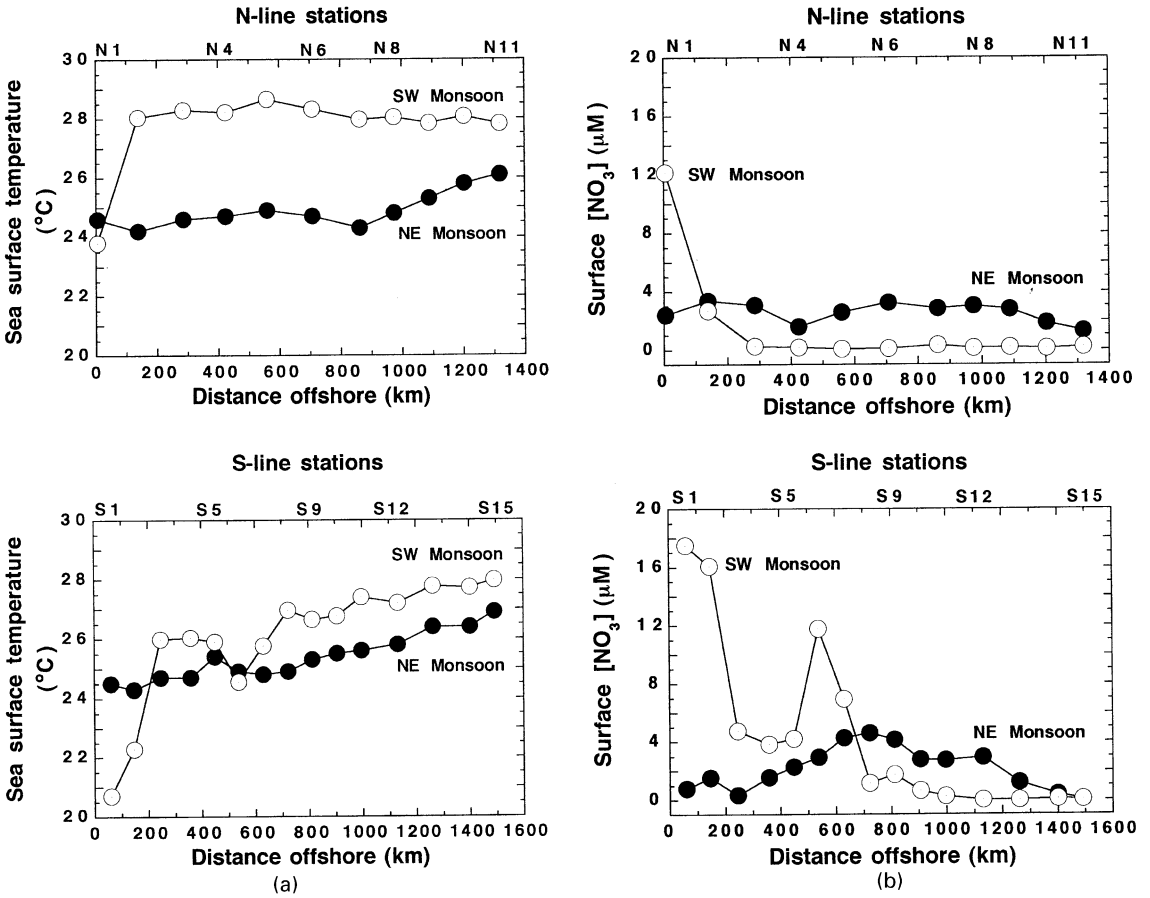

Fig. 2. Surface water properties at stations on the N- and S-lines during the 1995 NE and SW Monsoons (a) sea surface temperature (SST), (b) $[NO_3^-]$, and (c) percentage oxygen saturation. These values represent measurements or calculations for the mixed layer from the minimum CTD cast depth, nominally 1–2 m below the sea surface.

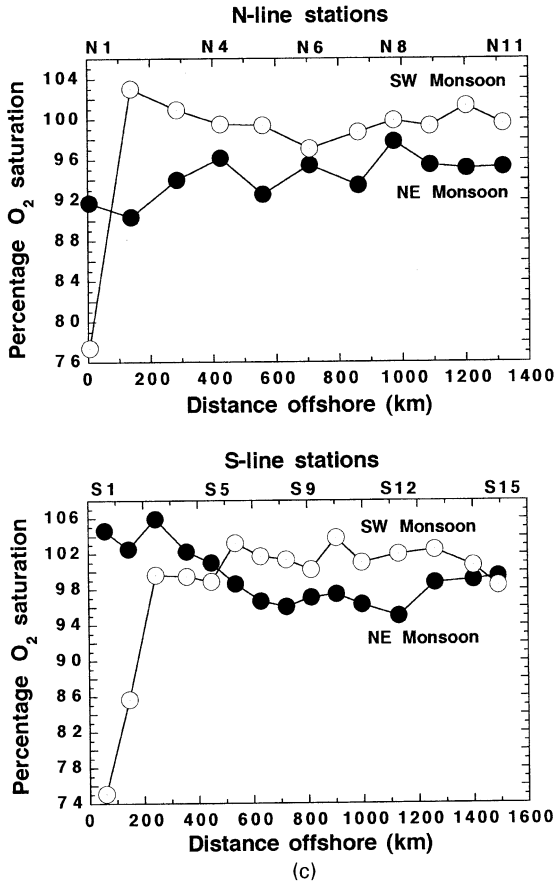

Fig. 2. (*continued*)

Examination of the production rate data and relationships between the various rate measurements revealed similarities among stations located close to the Omani coast and extending seaward on the S-line, which were different from the stations located further offshore. To differentiate between these two regimes, we grouped stations S2, S4 and S7 together and refer to them as the "nearshore stations", while stations N7, S11 and S15 were designated as the "offshore stations". At the nearshore stations diatoms were the dominant component of the phytoplankton assemblage in terms of abundance and carbon biomass (Garrison et al., 1998; Dennett et al., 1999) and relatively high $[NO_3^-]$ were measured there during both seasons. Conversely, the offshore stations had very low $[NO_3^-]$ during the SWM, but concentrations were similar to the nearshore sites during the NEM. During both monsoons, the phytoplankton community at the offshore locations was composed almost entirely of picoplankton (Garrison et al., 1998; Campbell et al., 1999). More detailed information regarding algal community structure, based on HPLC pigment analysis, has been presented by Latasa and Bidigare (1998). Their cluster analysis of pigment characteristics supports our separation of stations into a nearshore and offshore component, although station S11

Table 1
Comparison of mixed layer depths (MLD) and the depth of the 4% irradiance level (4% E_o) during the 1995 Northeast and Southwest monsoons. Mixed layer depths were calculated from a 0.125 kg m^{-3} change in density

Station ID	Northeast Monsoon		Southwest Monsoon	
	MLD[a] (m)	4% E_o (m)	MLD[a] (m)	4% E_o (m)
N7	70	73	52	61
S15	88	63	94	48
S11	96	38	74	46
S7	96	33	42	48
S4	80	36	62	32
S2	60	28	26	27

[a]Data provided courtesy of W. Gardner, TAMU.

had high concentrations of a senescent diatom marker and was more closely related to the nearshore, eutrophic sites than the oligotrophic ones during the late SWM (TN050).

3.2. Oxygen production and respiration rates

Profiles of gross and net O_2 production and daily respiration rates are shown for the NEM and SWM (Fig. 3). With the exception of station N7, very little vertical structure was evident in the net production profiles during the NEM (Fig. 3a). In contrast, a much stronger response to the submarine light field was seen during the SWM (Fig. 3b). During both monsoons gross photosynthetic rates were substantially > 0 at the 4% E_o, but in most instances the net community compensation depth (i.e., depth where daily net community production rate $= 0$) corresponded to the 4% E_o. Net production was $\geqslant 0$ throughout the euphotic zone, except at station N7 during the winter (NEM) when community respiration exceeded production at and below the 27% E_o. Comparison of depth-integrated gross production rates with depth-integrated dark community respiration rates at each of the intermediate stations during the SWM indicated that critical depths were situated below the 4% E_o. Overall, depth-averaged gross and net O_2 production rates were 52 and 42% higher during the SWM compared to the NEM (gross O_2: 7.9 ± 0.7 compared to $5.2 \pm 0.6\,\mu M\,d^{-1}$ and net O_2: 3.4 ± 0.5 compared to $2.4 \pm 0.4\,\mu M\,d^{-1}$). Assimilation numbers for light-saturated gross O_2 production rates averaged 1.5 ± 0.20 and $1.8 \pm 0.18\,\mu mol\,O_2$ (μg chl $a)^{-1}\,h^{-1}$ for the NEM and SWM, respectively.

Daily respiration rates tended to be highest in the upper water column and decreased with depth (Figs. 3a, b). Rates ranged from -1 to $-8\,\mu MO_2\,d^{-1}$ and were a function of gross production (Fig. 4). Mean daily respiration rates during the SWM were 50% higher than the NEM (-4.5 ± 0.3 versus $-3.0 \pm 0.3\,\mu M\,d^{-1}$, respectively), coinciding with higher rates of gross production in the summer (SWM). In contrast, dark respiration rates during the SWM averaged $-2.4 \pm 0.15\,\mu M\,O_2\,d^{-1}$ and were independent of net production (Fig. 5a).

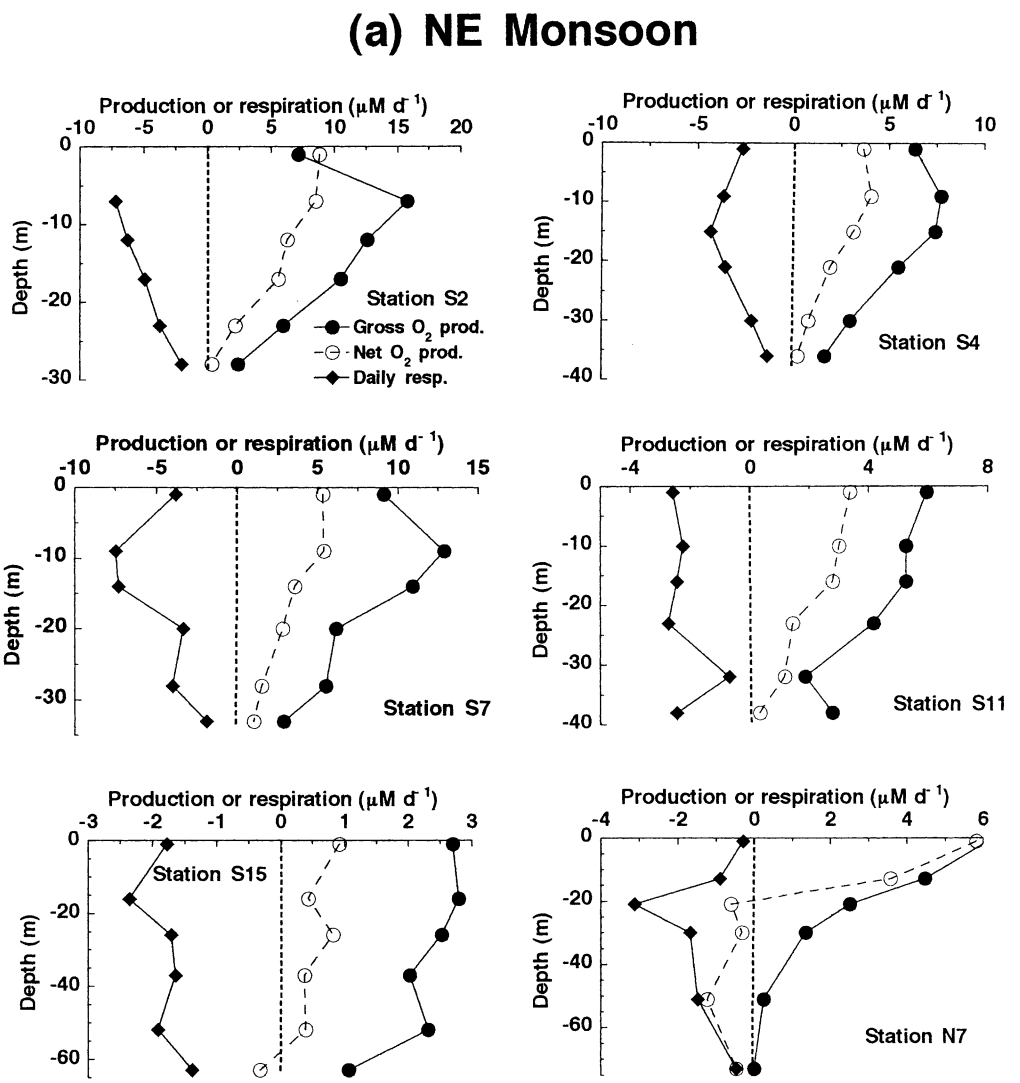

Fig. 3. Profiles of gross and net O_2 production and daily respiration rates ($\mu M\ O_2\ d^{-1}$) measured in situ during the (a) NE and (b) SW Monsoons.

At low net O_2 production rates ($\leqslant 1\,\mu M\,d^{-1}$), dark respiration/net production ratios exhibited a broad range of values, between 0.7 and 35, with ratios dramatically increasing at the lowest production levels (Fig. 5b). At the highest net production rates, 10 to $13\,\mu M\,O_2\,d^{-1}$, dark respiration accounted for $\sim 20\%$ of net production. At low rates of net production, and $[NO_3^-] < 1\,\mu M$, the ratio varied by an order of magnitude, from 0.5 to ~ 5 (Fig. 5c). With the exception of one station, dark respiration rates were $27 \pm 5\%$ of light-saturated net production when surface $[NO_3^-] > 1\,\mu M$.

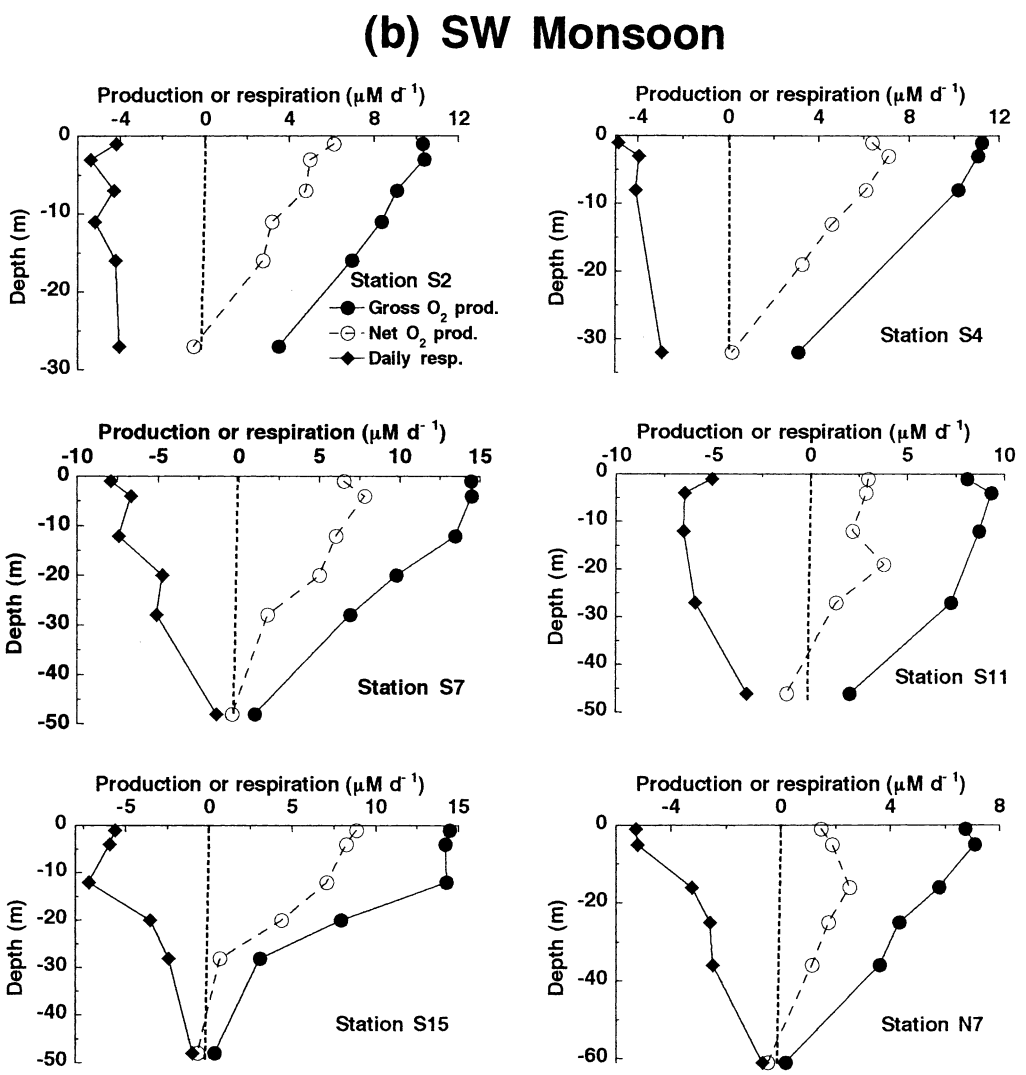

Fig. 3. (*continued*)

3.3. Net oxygen and "new" production rates

Net O_2 production rates were compared to the decrease in $[NO_3^-]$ (i.e., $\Delta[NO_3^-]$) in quartz bottles incubated for 24 h (Fig. 6). The slope of regression lines for the in situ incubations at the long stations were 10.9 ± 1.5 (NEM) and 7.9 ± 1.3 (SWM) (Fig. 6a). Deck incubations carried out at the intermediate stations had net $O_2/\Delta[NO_3^-]$ ratios that were higher than their in situ counterparts: 13.1 ± 1.4 (NEM) compared to 9.9 ± 0.2 (SWM) (Fig. 6b). At the 95% confidence limit, none of

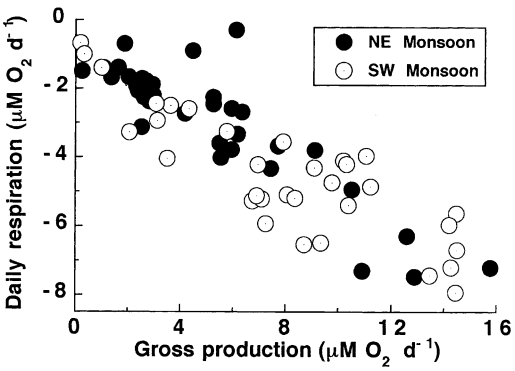

Fig. 4. Daily respiration rates as a function of gross O_2 production. Regression equations for the NE and SW Monsoons are $Y = -0.69–0.43X$ and $Y = -1.68–0.36X$, respectively.

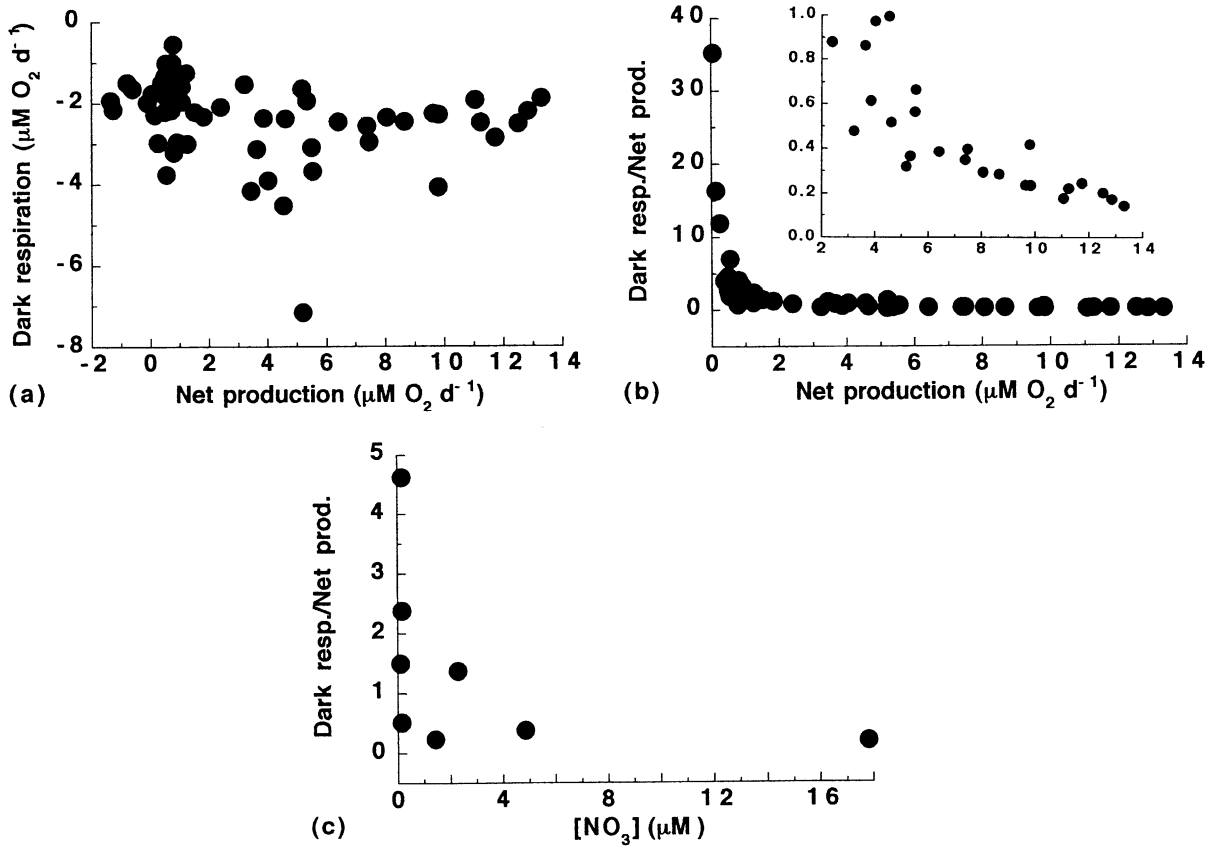

Fig. 5. (a) Dark respiration rates as a function of net O_2 production during the SW Monsoon, (b) dark respiration/net O_2 production ratios expressed as a function of net production. Inset shows ratios when net production is $\geqslant 2\,\mu M\,O_2\,d^{-1}$ and (c) dark respiration/net O_2 production ratios as a function of the $[NO_3^-]$.

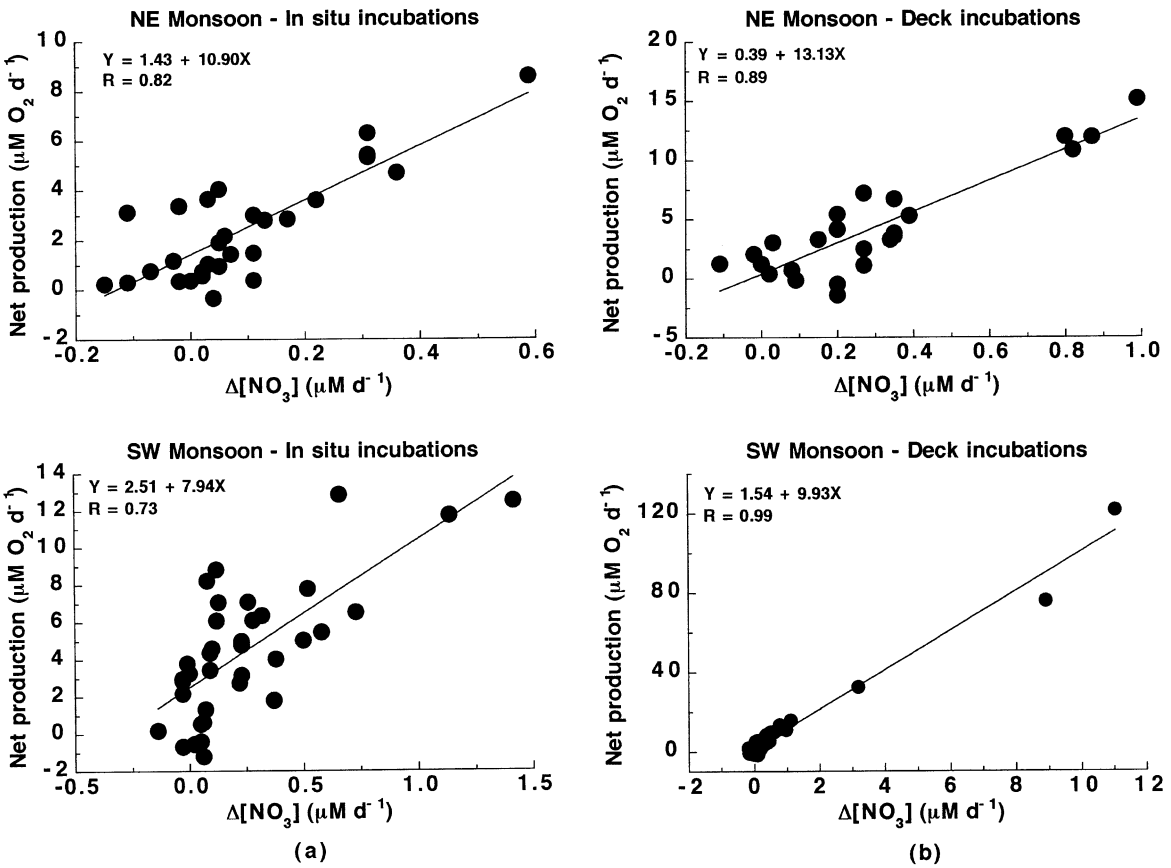

Fig. 6. Comparison of net O_2 production and new production determined by the decrease in the $[NO_3^-]$ measured during (a) in situ incubations at the long stations and (b) deck incubations at the intermediate stations for the NE and SW Monsoons.

these values were different from each other or the Redfield ratio of 10.6 for O_2/N (Anderson and Sarmiento, 1994). At the long stations, net O_2 production rates in the deck incubators were 19 and 21% higher than in situ rates for the NEM and SWM, respectively, due to an over collection of incident radiation (Barber et al., 1997).

Comparison of the net and new production data also revealed net O_2 production when $\Delta[NO_3^-] = 0$. New production in the bottles due to nitrogen fixation cannot be ruled out, although 3 of the 4 intercepts were not different than the estimated experimental error of $\sim 1.4\,\mu M\ O_2$. Alternatively, some portion of net O_2 production may have been due to NH_4^+ assimilation. If that were the case, new and net production would have been uncoupled and not in steady-state over the 24 h incubation period. It is questionable whether the two production terms would have been as highly correlated over the wide range of ambient $[NO_3^-]$ observed.

Table 2
Integrated (to the 4% E_o) production rates during the 1995 Northeast (NE) and Southwest (SW) monsoons[a]

Station ID	24 hour Gross C	24 hour Net C	12 hour ^{14}C	24 hour ^{14}C	24 hour total ^{15}N	24 hour $^{15}NO_3$
NE Monsoon:						
N7	115.0	30.8	104.4	86.1	148.3	12.1
S15	127.5	20.8	60.0	46.0	84.5	13.4
S11	130.8	57.5	83.2	66.3	91.8	18.9
S7	230.0	81.7	104.8	81.0	98.2	14.1
S4	164.2	61.7	85.7	72.9	96.6	11.0
S2	225.8	114.2	129.7	106.7	123.2	23.1
$\bar{X} \pm$ SE	166 ± 21	61 ± 14	95 ± 10	77 ± 8	107 ± 10	15 ± 2
SW Monsoon:						
N7	205.0	54.2	93.4	79.7	120.7	14.3
S15	275.8	115.0	147.2	129.6	261.2	56.4
S11	275.0	52.5	150.0	120.3	ND	30.0
S7	338.3	120.8	140.9	126.9	777.5	17.9
S4	198.3	90.0	118.5	100.2	33.7	9.6
S2	166.7	56.7	83.6	69.7	64.0	7.8
$\bar{X} \pm$ SE	243 ± 26	82 ± 13	122 ± 12	104 ± 10	120 ± 50	23 ± 7

[a]Station locations are given in Fig. 1. All production rates have units of mmol C m^{-2} $time^{-1}$. Data from station S7 was excluded from the calculation of mean 24 hour total ^{15}N production during the SW Monsoon. ND = no data.

3.4. Integrated carbon production

Overall, daily gross C production was 46% higher during the SWM (243 ± 26 mmol C m^{-2} d^{-1}; range: 167–338 mmol C m^{-2} d^{-1}) compared to the NEM (166 ± 21 mmol C m^{-2} d^{-1}; range: 115–230 mmol C m^{-2} d^{-1}) (Table 2). Onshore-offshore gradients in production were evident for both monsoons, although they were much stronger for the NEM (Fig. 7). In both seasons, gross production rates were highest at station S7. In the winter (NEM), gross production was higher close to the coast and decreased with increasing distance offshore. Gross production averaged 207 ± 21 mmol C m^{-2} d^{-1} at the coastal stations compared to 124 ± 5 mmol C m^{-2} d^{-1} farther offshore, while net production was 86 ± 15 and 36 ± 11 mmol C m^{-2} d^{-1} at the two sites. In the SWM, gross production rates were generally lower close to the coast and increased slightly with distance from shore but were not significantly different between coastal (234 ± 53 mmol C m^{-2} d^{-1}) and offshore sites (252 ± 23 mmol C m^{-2} d^{-1}). In contrast, net C production was somewhat higher at the nearshore stations (89 ± 19 mmol C m^{-2} d^{-1}) than the offshore ones (74 ± 21 mmol C m^{-2} d^{-1}).

In the two monsoons, 12 and 24 h ^{14}C production seriously underestimated gross C production (Table 2). The fixation of ^{14}C during the photoperiod was 57 and 50% of gross C production for the

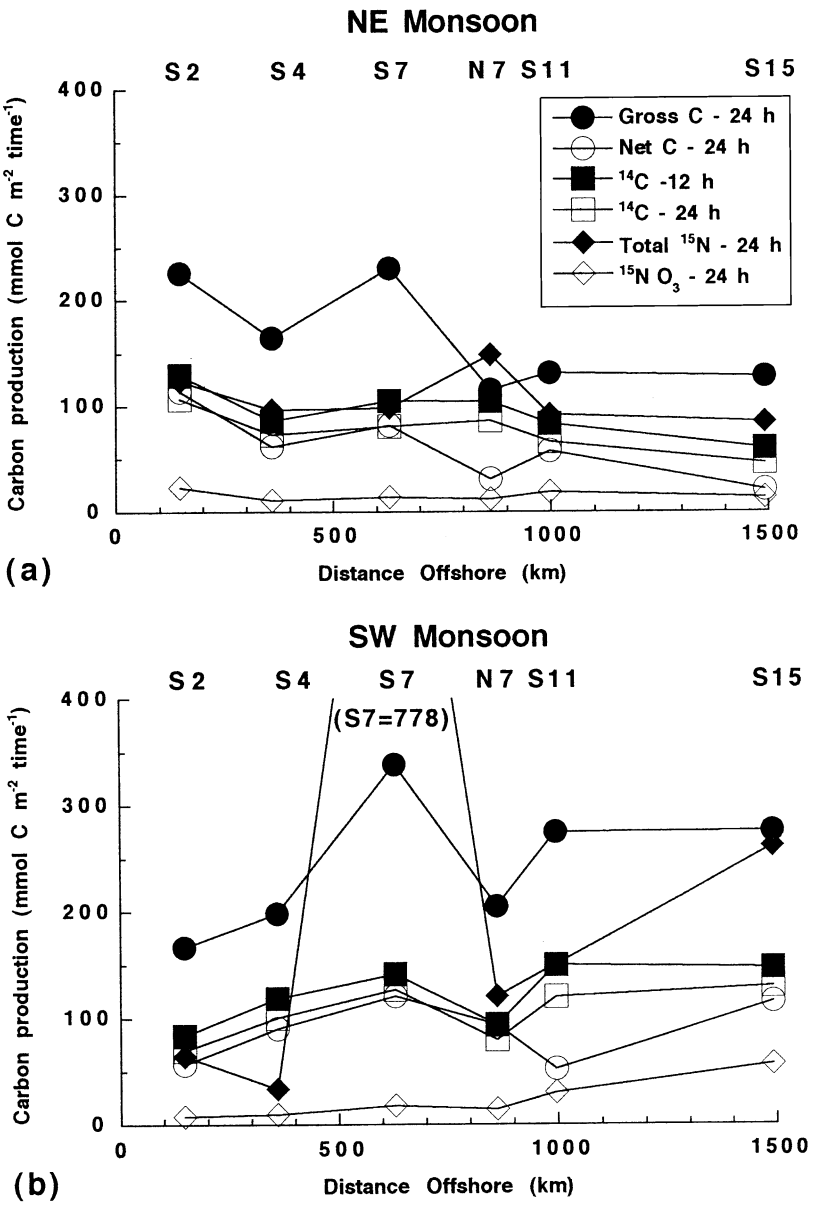

Fig. 7. Spatial distribution of carbon production integrated to the 4% irradiance level during the (a) NE and (b) SW Monsoons.

NEM and SWM. Thus, by the end of the photoperiod roughly half of the newly fixed carbon had been metabolized. However, ^{14}C fixation was approximately equal to gross C production at station N7 during the NEM, being 91% of gross C production at the end of the photoperiod and 75% after 24 h. Overnight losses of $PO^{14}C$ were similar for the two seasons, averaging 7 to 11% of gross C production.

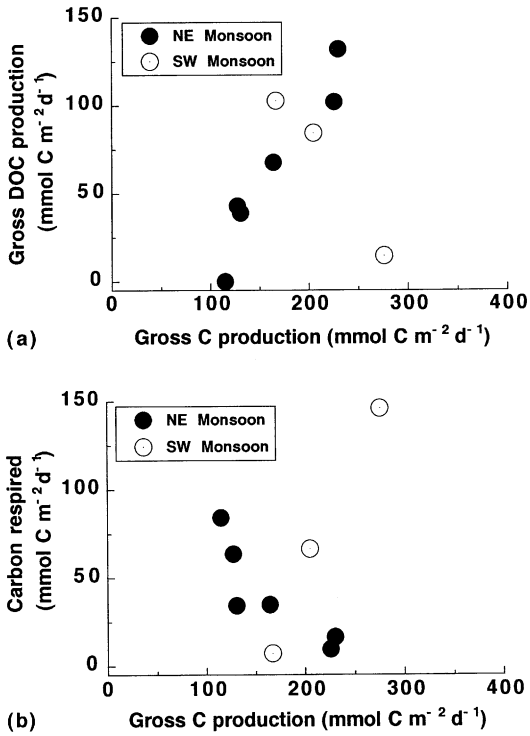

Fig. 8. (a) Gross dissolved organic carbon production as a function of gross C production and (b) the amount of metabolized gross C production respired as a function of gross C production during the NE and SW Monsoons.

During the NEM, net C, ^{14}C and total ^{15}N production did not differ appreciably among the coastal stations, (Fig. 7a). Farther offshore, ^{14}C and total ^{15}N production were between gross and net C production, except at N7 where total ^{15}N production exceeded gross production. New production was $18 \pm 0.9\%$ of net C production at the nearshore stations and $46 \pm 10\%$ at the offshore stations (Table 2).

In the SWM, daily ^{14}C production was the same as net C production across the transect (Fig. 7b). Total ^{15}N assimilation was between gross C and net C production at most stations, although it was two-fold greater than gross C production at station S7 due to high rates of regenerated production (Table 2).

Carbon respiration and gross DOC production were both a function of gross C production during the NEM (Fig. 8). Gross DOC production increased linearly in response to higher production rates, whereas carbon respiration was inversely related to gross C production. As a result of this dependence, two different patterns of carbon metabolism emerged for the nearshore and offshore stations (Fig. 9a). The nearshore stations were characterized by high net C/gross C ratios (0.36–0.51), indicating a large proportion of gross production was retained as net production (Table 2). Of the gross production that was metabolized, between 41 and 57% ended up in the DOC pool compared to 4–21% that was respired. The offshore stations were generally distinguished by lower production rates and had respiration rates that were similar to or surpassed

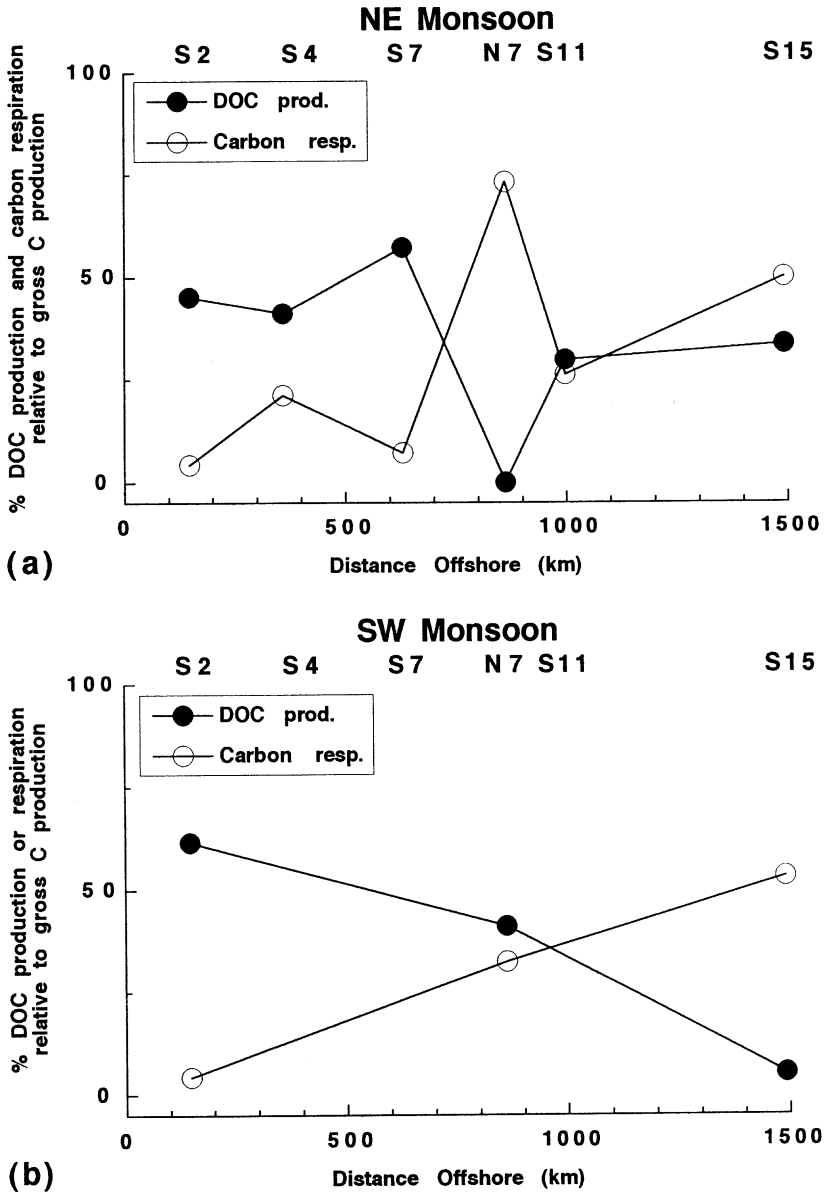

Fig. 9. Distribution of metabolized gross C production into respiratory (autotrophic and heterotrophic) and dissolved pools expressed as a percentage of gross C production during the (a) NE and (b) SW Monsoons.

gross DOC production rates. Net C production rates were low at these stations because more gross production was metabolized, as was evident in the lower net C/gross C ratios (0.16–0.44). During the NEM, gross DOC production at the nearshore stations averaged $100 \pm 19\,\mathrm{mmol\,C\,m^{-2}\,d^{-1}}$ compared to $27 \pm 14\,\mathrm{mmol\,C\,m^{-2}\,d^{-1}}$ at the three offshore sites. In contrast, respiration

Table 3
Partitioning of gross C production into carbon respiration and gross and net DOC production during the 1995 NE and SW monsoons[a]

Station ID	Gross C prod.lost	Gross DOC prod.	Resp.	Net DOC prod.	% Gross DOC prod.	% Resp.	% Net C prod.
NE Monsoon:							
N7	84.2	0.0	84.2	18.7	0.0	73.2	26.8
S15	106.7	43.0	63.7	7.4	33.7	50.0	16.3
S11	73.3	39.0	34.3	38.6	29.8	26.2	44.0
S7	148.3	131.8	16.5	67.6	57.3	7.2	35.5
S4	102.5	67.6	34.9	50.7	41.2	21.3	37.6
S2	111.6	102.0	9.6	91.1	45.2	4.3	50.6
$\bar{X} \pm SE$	104 ± 11	64 ± 19	41 ± 12	46 ± 13	35 ± 8	30 ± 11	35 ± 5
SW Monsoon:							
N7	150.8	84.3	66.5	39.9	41.1	32.4	26.4
S15	160.8	14.6	146.2	58.6	5.3	53.0	41.7
S11	222.5	ND	ND	22.5	ND	ND	19.1
S7	217.5	[b]	[b]	102.9	[b]	[b]	35.7
S4	108.3	[b]	[b]	80.4	[b]	[b]	45.4
S2	110.0	102.7	7.3	48.9	61.6	4.4	34.0
$\bar{X} \pm SE$	162 ± 20	67 ± 27	73 ± 40	59 ± 12	36 ± 16	30 ± 14	34 ± 4

[a]Station locations are given in Fig. 1. Data in columns 2, 3, 4 and 5 have units of mmol C $m^{-2} d^{-1}$. Percentages of gross DOC production, carbon respiration and net C production are expressed relative to gross C production. ND = no data.
[b]indicates that a calculation could not be made because gross DOC production was greater than the total amount of metabolized production.

consumed approximately three times more carbon (61 ± 14 versus 20 ± 8 mmol C $m^{-2} d^{-1}$) in the offshore waters than at the stations nearer to shore (Table 3).

It was not possible to partition metabolized gross C production into respiration and dissolved production at S4 and S7 during the SWM. At those stations gross DOC production was greater than the total amount of metabolized gross C production and they were omitted from the analysis (Table 3). As a result, gross DOC production and respiration were not well constrained as a function of gross C production (Fig. 8). The trend in the data suggests that the relationships observed between respiration and gross DOC production with gross C production were opposite of those found during the NEM. This was due to higher rates of gross C production encountered at the offshore stations during the SWM. Interestingly, the same onshore–offshore pattern for the partitioning of metabolized gross production was found for the two monsoons; high DOC production rates in nearshore, diatom-dominated waters and the dominance of respiratory metabolism further offshore in picoplankton-rich communities (Fig. 9b). This indicates that the partitioning of production is independent of the absolute amount of gross production but is most likely determined by community composition and food web structure. Gross DOC production was

highest at stations N7 and S2, accounting for 41 and 62% of gross C production (Table 3). Overall, there was no difference in gross DOC production for the two monsoons (64 ± 19 versus $67 \pm 27\,\mathrm{mmol\,C\,m^{-2}\,d^{-1}}$) (Table 3).

4. Discussion

In this study we investigated the response of the biological community to the broad range of physical forcing that characterizes the Arabian Sea. In the summer (SWM), MLDs and the depth of the 4% E_o were relatively shallow compared to the NEM (Table 1). Using in situ observations from a moored array, Dickey et al. (1998) found the maximum MLD was deeper in the winter (110 m) than the summer (80 m) because of a negative net surface heat flux in the NEM versus a positive heat gain during the SWM. At the mooring site, depth-integrated chlorophyll *a* biomass and primary production were inversely related to the MLD (Marra et al., 1998). The biological response to monsoonal forcing manifested itself in the form of elevated production and daily respiration rates (Table 2). Increased biological production, deduced from export flux studies, distinguishes the SWM, with it making the largest contribution to annual carbon export from the euphotic zone (Haake et al., 1993; Buesseler, 1998). In this study, integrated daily gross C production was 46% higher during the SWM compared to the NEM, while net C production increased by 34%, 12 and 24 h ^{14}C production by 28–35%, total ^{15}N production by 12% and new production by 53% (Table 2).

Past work explained spatial heterogeneity in primary production as being due to variations in monsoonal strength affecting circulation dynamics and the distribution of nutrients (Brock et al., 1994). Onshore–offshore differences in production rates during the NEM did not appear to be related to the distribution of macronutrients (Figs. 2b and 7a). Higher rates of gross C and net C production were correlated with high $[NO_3^-]$ at the nearshore stations; however, lower production rates at offshore sites coincided with both high and extremely low $[NO_3^-]$. In addition, relationships between the various production parameters at the nearshore (i.e., net C = ^{14}C = total ^{15}N production) and offshore stations (i.e., ^{14}C and total ^{15}N were between gross and net C production) were not correlated to phytoplankton growth rates (Landry et al., 1998; Caron and Dennett, 1999). Culture experiments and modeling studies (DiTullio and Laws, 1986; Williams, 1993b) suggest that ^{14}C equals net production when phytoplankton growth rates are $> 0.5\,\mathrm{d^{-1}}$, but is between gross and net production when growth rates are lower. Our data suggest that heterotrophic metabolism affected the various production measurements enough to obscure any connection between phytoplankton growth and production.

The production-nutrient relationships for the SWM are more difficult to reconcile, given the high rates of gross production in the offshore regions (Fig. 7b). For instance, gross O_2 production rates at the offshore stations were an order of magnitude higher than rates measured in the oligotrophic subtropical gyre of the North Pacific Ocean (Williams and Purdie, 1991). Part of this difference can be explained by higher chlorophyll *a* concentrations in the Arabian Sea than the subtropical Pacific Ocean (0.5 versus $< 0.1\,\mathrm{mg\,m^{-3}}$). Since ambient $[NO_3^-]$ were on the order of 0.1 μM during our occupation of the stations, nutrient regeneration must have been rapid enough to meet the nutritional requirements of the phytoplankton (McCarthy and Goldman, 1979) and fuel the high rates of gross production we measured. These results and others (Marra and

Heinemann, 1987; Laws et al., 1987) demonstrate that oligotrophic regions may not always be characterized by low biomass and production rates and that our understanding of oceanic processes is limited when viewed as a series of brief snapshots.

Seasonal and spatial differences in integrated production were not apparent when gross C production was normalized to the chlorophyll *a* concentration. Light-saturated assimilation numbers for gross O_2 production rates were 75 (NEM) and 90% (SWM) of the theoretical maximum for photosynthetic indices under nutrient-replete conditions (Falkowski, 1981). It is unlikely that such high assimilation numbers would have been observed if the phytoplankton were nutrient-limited. For example, recent measurements of gross O_2 production rates under oligotrophic conditions produced gross O_2/chl *a* values between 0.2 and 1 μmol O_2 $(\mu g\,\mathrm{chl}\,a)^{-1}\,h^{-1}$ (Hitchcock et al., 1999). These values are the same as photosynthetic indices from the oligotrophic subtropical gyre in the North Pacific Ocean (Williamys and Purdie, 1991). The high assimilation numbers obtained in this study indicate that gross primary production was not severely nutrient-limited during either monsoon, even when the ambient $[NO_3^-]$ was quite low. Comparison of phytoplankton growth rates measured in unenriched and enriched dilution experiments led Caron and Dennett (1999) to reach the same conclusion for the NEM. Measurements made later in the SWM (TN050) than our cruise found no evidence of nutrient-limited phytoplankton growth at the nearshore stations although there were indications of limited growth further offshore (Landry et al., 1998).

On the other hand, one can make the case for nutrient-limited production in this study on the basis that high dark respiration/net production ratios in light-saturated samples coincided with low $[NO_3^-]$ (Fig. 5). Dark respiration rates are generally thought to account for 10% of light-saturated photosynthetic rates (Parsons et al., 1984). Dark respiration/net production ratios > 0.5 have been interpreted as being representative of nutrient-limited conditions (Ryther, 1954; Osborne and Geider, 1986). Given the strong evidence for nutrient sufficiency in the foregoing discussion, the high respiration/production ratios were probably due to heterotrophic metabolism rather than nutrient-limited phytoplankton growth. As a result of the inclusion of heterotrophic respiration in net community production measurements, the usefulness of these ratios as an index of phytoplankton nutrient sufficiency is limited for most field applications, with the possible exception of bloom events.

4.1. Respiration in the light and the dark

The dark component of respiration in the light is believed to be important for providing carbon skeletons and reductant for carboxylation processes. Higher respiration rates in the light support the increased supply of substrates required for photosynthesis and also may provide additional energy to supplement photosynthesis (Geider and Osborne, 1989). Early studies demonstrated that dark respiration rates were not inhibited in the light but enhanced under illuminated conditions (Peltier and Thibault, 1985). Weger et al. (1989) found mitochondrial respiration rates in the light were twice those in the dark. Much of the evidence to date suggests that photoenhanced mitochondrial respiration is responsible for most of the respiratory activity in the light. Other respiratory processes limited to the photoperiod, notably photorespiration, chlororespiration and the Mehler reaction, appear to play a minor role in phytoplankton respiratory metabolism (Falkowski and Owens, 1978; Raven and Beardall, 1981; Weger et al., 1989). The high rates of gross DOC production we have estimated (Tables 2 and 3) suggest that photorespiration may have been

a major sink for gross production in the Arabian Sea. However, we cannot rule out the role of grazers in mediating the release of production into the dissolved pool.

In the summer (SWM), daily respiration rates were, on average, almost twice dark respiration rates (-4.5 versus $-2.4\,\mu M\,O_2\,d^{-1}$). Daily respiration rates were clearly a function of gross photosynthesis (Fig. 4), unlike dark respiration rates (Fig. 5a). As a result of higher gross C production, daily respiration rates during the SWM were 50% higher than the NEM. These results are analogous to those of Kiddon et al. (1995) who proposed that daily respiration rates consist of two components. The first is proportional to the production rate and represents the percentage of newly fixed carbon respired in 24 h. For the North Atlantic Bloom Experiment (NABE) daily respiration was $35 \pm 6\%$ of gross O_2 production. Similar values were found for the NEM (43%) and SWM (36%), derived from the slope of the regression lines in Fig. 4. These values also agree with the amount of ^{14}C respired relative to gross C production in 24 h (NEM: $48 \pm 6\%$ and SWM: $43 \pm 2\%$) (Table 2). Slightly more newly fixed carbon was utilized in the NEM than the SWM. The second component of daily respiration is independent of production (i.e., there is no depth dependence) and involves respiration of carbon fixed prior to the same day's photoperiod. In the NABE, Kiddon et al. (1995) obtained a value of $-1.54\,\mu M\,O_2\,d^{-1}$ that is close to $-1.68\,\mu M\,O_2\,d^{-1}$ for the SWM. This latter number is lower than, but not different from, the average dark respiration rate of $-2.41 \pm 1.1\,\mu M\,O_2\,d^{-1}$.

Daily ^{14}C production underestimated gross C production by approximately 50% during the two monsoons (Table 2). Comparable values have been found in the North Atlantic Ocean (Bender et al., 1992) and the equatorial Pacific Ocean (Bender et al., 1999). Metabolic processes that account for these differences include autotrophic and heterotrophic mitochondrial respiration, light respiration by phytoplankton and DOC production (Bender et al., 1999). In this study, the turnover of $PO^{14}C$ occurred primarily during the photoperiod, with smaller losses incurred overnight (Table 2). Four times more $PO^{14}C$ was lost during the photoperiod compared to overnight during the NEM versus a seven-fold difference in the SWM. Dark ^{14}C respiration was between 7 and 11% of gross photosynthesis with no discernible onshore-offshore pattern related to the phytoplankton species composition. These values are lower than the 25% reported by Falkowski and Owens (1978). Overnight losses of $PO^{14}C$ were $19.4 \pm 1.3\%$ (NEM) and $14.7 \pm 1.4\%$ (SWM) of photoperiod uptake and are within the range determined for phytoplankton respiration in culture studies (Laws and Wong, 1978).

4.2. DOC production

Particulate ^{14}C production can either be respired as CO_2 or lost as DOC. The discrepancy between gross C and particulate ^{14}C production or between gross and net C production only provides information on the total amount of production that was metabolized and nothing about the contribution of respiratory and dissolved production to carbon metabolism. Gross production should be equivalent to total production estimated from ^{15}N uptake measurements (Platt and Sathyendranath, 1993; Williams, 1993a). With the exception of one station during each monsoon, total ^{15}N uptake seriously underestimated gross production (Table 2). Given the fairly good agreement between net O_2 production and $\Delta[NO_3^-]$ in the quartz incubation bottles (Fig. 6), we interpret the discrepancy between gross and total production being due to the loss of ^{15}N label to the dissolved organic pool. Bronk et al. (1994) reported that the production of $DO^{15}N$ in NH_4^+

uptake experiments reduced gross N production by 25% compared to 41% for NO_3^-. When NH_4^+ and NO_3^- are considered together, total N uptake underestimated gross N production by 52 and 22% at a coastal and oceanic site, respectively (calculated from Table 1, Bronk et al., 1994). From these data we might expect the loss of ^{15}N label to the dissolved pool to be more of a problem when NO_3^- is the major nitrogen source, such as in upwelling regions. In this study, total ^{15}N production (scaled to carbon) underestimated gross C production by $48 \pm 5\%$ at the nearshore stations and $32 \pm 2\%$ at the offshore ones during the NEM compared to $72 \pm 11\%$ and $23 \pm 18\%$ during the SWM (Table 2).

In general, DOC production accounts for 0–30% of net production (Norrman et al., 1995). In a cross-system analysis, Baines and Pace (1991) found that extracellular release increased linearly as a function of net production and that, on average, 13% of fixed ^{14}C was released as DOC. Those values are much lower than estimated in this study, possibly because extracellular release rates in the original studies were significantly underestimated due to heterotrophic utilization of the excreted photosynthate during the incubation. In a series of ^{14}C-labeling experiments, heterotrophic uptake of dissolved compounds led to DOC production being underestimated by up to 60% (Lancelot, 1979).

We used the difference between gross C and total ^{15}N production and net C and new (i.e., $^{15}NO_3$) production to estimate gross and net DOC production (Table 3). This approach will overestimate gross DOC production if the uptake rates of all the major nitrogen sources are not included in the total N production measurement. Likewise, net DOC production will be overestimated if nitrogen fixation is significant but not included in new production. During the NEM, nitrogen uptake measurements included NO_3^-, NH_4^+ and NO_2^-, but not urea. Urea can account for 10–30% of total N uptake in coastal waters (McCarthy et al., 1977; Probyn, 1985) and up to 57% in oligotrophic regions (Eppley et al., 1977; Price and Harrison, 1987). Higher rates of gross C production relative to total N uptake at the nearshore sites resulted in high rates of gross DOC production. Assuming DOC production was overestimated by 30% at the nearshore sites and 60% offshore, gross DOC production is reduced from 100 to 70 mmol C m^{-2} d^{-1} and from 27 to 11 mmol C m^{-2} d^{-1} in each of those regions, respectively. This correction causes absolute gross DOC production rates to decrease but the spatial pattern is unaffected; high dissolved production in nearshore waters and lower rates offshore.

Our estimate of DOC production also will be affected by the nitrogen sources (inorganic versus organic) used by the bacteria and the rate at which dissolved organic nitrogen (DON) was metabolized during the ^{15}N incubations. Although heterotrophic bacteria are a major sink for DON in marine systems (Azam and Hodson, 1977; McCarthy et al., 1998), dissolved amino acid production and uptake can be substantially less than the bacterial growth rate, indicating a reliance on some other nitrogen substrate. Heterotrophic bacteria mainly use NH_4^+ (Wheeler and Kirchman, 1986) when amino acid concentrations are too low to support bacterial growth (Kirchman et al., 1989). In most cases, the assimilation of NO_3^- and urea by bacteria is negligible (Wheeler and Kirchman, 1986). The exception occurs when bacterial turnover of the DOC pool is rapid, such as during phytoplankton blooms, and heterotrophic bacteria meet their nitrogen requirements by preferentially assimilating dissolved inorganic nitrogen instead of DON (Kirchman et al., 1991). At these times the cycling of the DOC and DON pools are uncoupled, with the turnover of the DON pool being much slower. The incorporation of significant amounts of ^{15}N-labeled compounds into bacterial biomass would have caused total N and new production to be overestimated. No data

were available with which to evaluate the magnitude of this potential problem, but it offers an explanation as to how total ^{15}N production could be greater than gross production at station S7 during the SWM (Fig. 7b).

We have no evidence that the high DOC production rates were an artifact of improper handling or processing of the samples, although we cannot absolutely rule out the possibility that methodological effects may have compromised the data. For instance, care was taken to ensure that the phytoplankton assemblage was not light shocked during sampling or the addition of label, ^{15}N incubation times were kept short (i.e., 4–6 h), and the ^{14}C and ^{15}N samples were filtered under low vacuum pressure to minimize cell lysis. Based on light-saturated gross O_2 assimilation numbers, it is unlikely that either light limitation (Zoltnik and Dubinsky, 1989) or nutrient stress (Ittekkot et al., 1981; Goldman et al., 1992; Smith et al., 1998) were responsible for the release of DOC, at least in samples in the upper euphotic zone. At deeper depths, differences in the spectral quality of light reaching the incubators may have caused more dissolved production to be released from the incubator samples. However, at low irradiances ($< 10\%$ E_o), Smith and Herman (1991) found that DOC production was two-fold *lower* in samples from the incubators compared to those in situ, even though both sets of samples were incubated under spectrally similar conditions.

Differences in the spectral quality of the incubation bottles may have played a role in biasing the data. Quartz incubation bottles were used for the oxygen production measurements, whereas ^{14}C incubations were carried out in polystrene tissue flasks and polycarbonate bottles were used for the ^{15}N measurements. Quartz is optically clear whereas polystrene and polycarbonate are not. Examination of vertical profiles of $^{18}O/^{14}C$ production rates tabulated from this data set revealed higher ratios in samples incubated just below the sea surface (0.62) compared to optical depths > 3 (0.31) (Laws et al., 2000). This difference was attributed to UV radiation reducing ^{18}O production to a greater extent than ^{14}C. If this same effect occurred in the ^{15}N samples, it would have been limited to bottles incubated at the highest light level(s) and caused ^{15}N production to be slightly elevated relative to gross production, not less. Spectral differences in the incubators and incubation bottles do not appear to have been in the proper direction to have produced enhanced rates of excellular release. Nonetheless, a thorough examination of the role that methodological factors play in accounting for differences between the various production measurements is warranted.

Extracellular release rates increased linearly in response to increasing production rates during the NEM (Fig. 8). This relationship also has been observed in culture and field studies (Mague et al., 1980; Zoltnik and Dubinsky, 1989; Biddanda and Benner, 1997; Gosselin et al., 1997) and newly produced DOC has been found to accumulate during and after phytoplankton blooms (Williams, 1995; Carlson et al., 1994, 1998). Hansell and Carlson (1998) have shown that the production of semilabile DOC only occurs during periods of net community production. There is evidence that DOC production rates are determined by the composition of the phytoplankton community. Of four species studied under nutrient-replete conditions, the diatom *Skeletonema costatum* released the highest percentage of particulate carbon production into the dissolved pool (49%) while the cyanobacterium *Synechococcus bacillaris* excreted the least production (12%) (calculated from Table 2, Biddanda and Benner, 1997). During the NEM, a significant fraction of net DOC production ($79 \pm 5\%$ of ^{14}C production) was released at the nearshore stations where diatoms dominated the phytoplankton (Dennett et al., 1999). Further offshore, where picoplankton were abundant (Campbell et al., 1999), DOC production was lower ($32 \pm 13\%$) but still represented a sizeable fraction of fixed carbon released into the dissolved pool.

Net DOC production was more than half of daily ^{14}C production (NEM: $56 \pm 12\%$, SWM: $58 \pm 10\%$). Hansell and Carlson (1998) also found that a high fraction of net community production accumulates as DOC (59–70%) in the Sargasso Sea during the spring bloom. Large increases in DOC concentrations in the Sargasso and Arabian Seas (especially during the NEM) led Hansell and Peltzer (1998) to conclude that deep mixing at both sites may favor biological communities that release DOC under those conditions. Unfortunately, there are no DOC production rate data available from the Arabian Sea Process Study with which to compare our results. Qualitatively, our Arabian Sea data agree with other observations that have suggested regions with high rates of net community production also have high rates of net DOC production and that upwelling areas are the most important sites globally for this process (Hansell and Carlson, 1998).

4.3. Partitioning of production

Whether production ends up as DOC or CO_2 can have important consequences for carbon storage in the ocean. By estimating the amount of gross C production partitioned into respiratory and dissolved organic pools, we conclude different pathways dominated carbon metabolism, depending on the trophic organization of the plankton community (Figs. 8 and 9). Hansell and Peltzer (1998) observed large changes in organic carbon stocks during the late SWM (TN050) that they attributed to changes in DOC concentrations. They speculated that these changes were tied to changes in the trophic organization of the food web responsible for DOC production. Conversely, plankton respiration can significantly increase CO_2 concentrations in surface waters (Sambrotto and Langdon, 1994). Wanninkhof et al. (1997) estimated that planktonic respiration accounted for 80% of the increase in DIC concentrations at the end of the spring diatom bloom on the west Florida Shelf. At that time, the community was composed primarily of organisms $< 5\,\mu M$ in size and net production was scarcely net autotrophic (Hitchcock et al., 1999). Thus, the interactions between autotrophs and heterotrophs appear to be critical in determining whether an ecosystem is a sink or a source of CO_2 (Blight et al., 1995). In this study water column production was strongly net autotrophic during the mid-SWM, but measurements made in the late SWM of 1994 revealed that net community production was barely autotrophic at nearshore stations and strongly heterotrophic further offshore (Robinson and Williams, 1999). The extent to which this represents inter-annual variability is not known, although Hitchcock et al. (1999) have suggested that subtropical and tropical ecosystems may have the ability to shift from being net autotrophic to net heterotrophic on relatively short time-scales.

Respiration by the microbial community is responsible for most of the remineralization of organic matter in the ocean, with bacterial metabolism the major component of heterotrophic carbon flow (Williams, 1981; Cole et al., 1988). Phytoplankton respiration is generally regarded as being insignificant, but it can account for $> 60\%$ of gross photosynthesis (Geider, 1992). In this study, high daily respiration rates relative to dark community respiration and substantial losses of $PO^{14}C$ in the photoperiod suggest two things. First, autotrophic respiration may have been a considerable sink for gross production and represented a large fraction of total respiratory activity. Second, autotrophic respiration may introduce significant diel variablity into water column respiratory processes. Unfortunately, phytoplankton respiration cannot be measured directly in field studies due to our inability to physically separate autotrophic and heterotrophic organisms. To estimate algal respiration we applied depth-integrated daily respiration : gross

Table 4
Contribution of algal respiration to dark community respiration during the 1995 Southwest Monsoon[a]

Station ID	Gross O_2 production	Dark respiration	Algal respiration	% Algal respiration
N2	263.6	124.1	55.4	45
N4	163.3	126.7	34.3	27
S3	275.3	74.7	57.8	77
S9	556.0	100.1	116.8	>100
N6	109.3	66.1	36.1	55
N9	81.2	78.7	26.8	34
N11	285.7	105.3	94.3	90
S13	132.1	95.8	43.6	46

[a]Algal respiration was estimated by applying a $R:P = 0.21$ to diatom-dominated stations (N2, N4, S3 and S9) and a $R:P = 0.33$ to stations where picoplankton prevailed (N6, N9, N11 and S13). Information on the composition of the phytoplankton assemblage at each station was obtained from Garrison et al. (1998) and Latasa and Bidgare (1998). Daily depth-integrated respiration : gross production ratios (R : P) were taken from Langdon (1993). Gross production and respiration rate data are integrated to the 4% E_o and have units of mmol O_2 $m^{-2} d^{-1}$.

production ratios obtained from Langdon (1993) to production data collected at the intermediate stations (Table 4). Phytoplankton respiration amounted to 27–90% of dark community respiration during the mid-SWM when production rates were high. By way of comparison, algal respiration accounted for 7–29% of community respiration in the late SWM when the euphotic zone was predominately heterotrophic (Robinson and Williams, 1999).

Net C/gross C ratios provide information on the ability of an ecosystem to retain production and set an upper limit on the amount of production that can be exported from the euphotic zone. Approximately 35 and 34% of gross C production was kept as net C production during the NEM and SWM, respectively, and $\sim 65\%$ of gross production was metabolized (Table 2). Net C/gross C ratios for the NABE (40%) (Bender et al., 1992) and the equatorial Pacific Ocean in the fall (44%) and spring (52%) (Bender et al., 1999) are similar to those in the Arabian Sea. In terms of net C production there is also considerable overlap. Integrated production during the NEM (61 ± 14 mmol C $m^{-2} d^{-1}$) and NABE (42 ± 13) were lower than the SWM (82 ± 13) and the equatorial Pacific Ocean (fall: 90 ± 34 and spring: 79 ± 20). These data show that net C/gross C ratios as proxies for export production are not well constrained by net community production. Export/production ratios determined for the upper 100 m in the Arabian Sea are extremely low, <2–10%, most of the time (including the NEM) but increase to >15–25% in the late SWM (Buesseler, 1998). The discrepancy between these data and the net C/gross C ratios we calculate suggests that the respiration of organic matter below the euphotic zone (i.e., below the 4% E_o) likely plays a pivotal role in determining the flux of organic matter to the deep ocean.

Productive ecosystems are characterized by high net C/gross C ratios, indicating that a large percentage of gross production goes into biomass and is eventually exported. In systems where remineralization dominates, net C/gross C ratios and export production are low (Eppley and Peterson, 1979). During the NEM, the diatom-dominated nearshore stations retained more gross

C production as net C production, as indicated by the high net C/gross C ratios, and had higher rates of gross DOC production relative to respiration (Tables 2 and 3). At the offshore locations, respiration exceeded gross DOC production and these ecosystems were characterized by low rates of net C production and low net C/gross C ratios. Net C production was low because higher cumulative metabolic losses (respiration plus gross DOC production) reduced gross C production to a greater extent than at the more productive sites (Table 3). Therefore, it is the magnitude of respiration and gross DOC production *relative* to gross C production that establishes how much net C production is retained by an ecosystem, not the absolute rate of gross C production.

Similiarly, the absolute amount of gross production was not crucial in determining how metabolized gross C production was partitioned. During the SWM, even though extremely high rates of gross C production were measured at the offshore stations, the same pattern of respiration exceeding DOC production was observed there (Fig. 9). This suggests that the trophic organization of plankton communities may be key to determining how much production is retained by an ecosystem, as well as, the proportion of metabolized production that is released as CO_2 or DOC. For example, production of DOC can be substantially enhanced by the grazer-mediated release of dissolved compounds (Jumars et al., 1989). Strom et al. (1997) noted that the release of DOC from phytoplankton in the presence of various grazers was 4 to 6 times greater than from phytoplankton alone. The onshore–offshore distribution of gross DOC production during the NEM was similar to the pattern observed in microzooplankton grazing rates, being 2-4 times higher at coastal stations than oceanic sites (Caron and Dennett, 1999). Moreover, there is some evidence that food web processes also may be critical in controlling the distribution and availability of organic carbon in the ocean. The DOC pool is heterogeneous, consisting of refractory components that can take months or more to degrade and labile fractions that can turn over in days. Dissolved organic compounds derived from phytoplankton blooms are extremely labile, decomposing in days to weeks (Amon and Benner, 1994; Carlson et al., 1994; Amon and Benner, 1996), whereas refractory DOC may be a by-product of the microbial loop (Legendre and LeFevre, 1995).

In summary, gross and net C production, ^{14}C incorporation and ^{15}N assimilation rates were higher (12–53%) during the SWM relative to the NEM. Daily ^{14}C and total ^{15}N production rates, scaled to carbon, seriously underestimated gross C production. Presumably, this was due to the loss of labeled particulate organic matter either via respiration and/or the production of dissolved organic matter. The composition of the phytoplankton community, reflecting the trophic structure, appeared to be important in determining how much gross production was retained in the ecosystem and the proportion of metabolized production that was released as CO_2 and DOC. These findings are in agreement with a variety of other studies that also have suggested food web processes play a central role in controlling the availability and distribution of carbon in the ocean. Whether the relationships revealed in this study also apply to other marine ecosystems remains to be seen.

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