Nutrient flux fuels the summer primary productivity in the oligotrophic waters of the Gulf of Aqaba, Red Sea

OCEANOLOGIA, 47 (1), 2005.
pp. 47–60.

KEYWORDS
Diffusion model
Eddy diffusivity
Biological stress
Chlorophyll a
Thermohaline stratification

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Received 22 November 2004, revised 14 February 2005, accepted 21 February 2005.

Abstract

The thermohaline characteristics of the Gulf of Aqaba, Red Sea, depict a well-defined seasonal pattern of winter mixing from December to April and summer stratification from May to November. This thermohaline structure is a major controlling factor of the nutrient, chlorophyll a and primary productivity seasonal cycles. The nitrate and chlorophyll a concentration records generated down to 200 m at a vertical resolution of 25 m – weekly during 1994, 1995 and every two weeks from April 1997 through to December 2000 – are employed to assess the nitrogen flux across the summer thermocline of the Gulf of Aqaba. The flux calculations are based on a simple diffusion model that incorporates the physical stress eddy diffusivity factor K_z and a biological stress factor k. Both K_z and k are calculated using the Michaelis-Menten equation and the nitrate concentration gradient. The total nitrate flux of the Gulf of Aqaba during the seven summer months (May–November) is estimated at 0.52 mole N m^{-2}. In relation to established primary productivity values (75.5 g C m^{-2} (May November)$^{-1}$) and

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the generated chlorophyll a records, this yields an f fraction of new to total primary production of 0.50. This relatively high f value is discussed with respect to the geophysical characteristics of the Gulf of Aqaba and similar oceanic basins. The remaining 50% is accounted for by cross-sectional flow from the relatively nutrient-rich coral reef coastal habitat and rapid recycling, triggered by high irradiance and water temperature.

1. Introduction

Re-injection of nutrients in the euphotic zone of oligotrophic waters, which fuels primary production, has been one of the most important and fundamental questions facing oceanographic research (Jenkins & Goldman 1985). Several authors have proposed a flux from deep water across the thermocline as the major nutrient source for primary production during summer. Estimation of the nitrogen (the limiting nutrient) flux across the summer thermocline in particular has received substantial attention, yet it has always been a continuous debate. Models of the nutrient flux into the euphotic zone may range from simple diffusion models (McCarthy & Carpenter 1983, Platt et al. 1984) to time-dependent mixed-layer ones (Klein & Coste 1984). According to Fasham (1995), simple models, if properly built and managed, can be as powerful as the most sophisticated ones. Nevertheless, no model to date, irrespective of its degree of complexity, seems capable of making satisfactory predictions for every possible set of conditions. Altabet (1989) has pointed out that variation in the flux estimates between different authors for the same region can be as high as tenfold. This author also stated that basic questions regarding the nature of the physical transport and the time scale of the flux have not yet been resolved.

Primary productivity in aquatic environments represents the link between the physical (light, temperature and water dynamics), chemical (inorganic and organic nutrients) and biological (phytoplankton and higher trophic levels) components of the system. Quantitative studies of primary productivity are therefore of crucial importance for understanding natural trophic cycles. Direct measurements of primary productivity are, however, difficult and costly, and are therefore not frequently carried out (Shulenberger & Ried 1981), especially in oligotrophic waters. The most common method for measuring primary productivity involves the use of radioactive carbon, which limits such measurements to labs capable of dealing with radioactive wastes. Quantitative studies of phytoplankton biomass have been used by several authors as indicators of primary productivity. The only pigment common to all phytoplankton (Jeffrey 1980), chlorophyll a has been widely utilised to estimate primary productivity (Jamart et al. 1977, Shulenberger & Ried 1981, Chapman et al. 1987, Gowen et al. 1992, and many others). In employing this technique, however, one should be aware that different photosynthetic parameters lead to different phytoplankton chlorophyll *a* concentrations. Translating chlorophyll *a* concentrations into organic carbon or organic nitrogen uptake rates may therefore vary depending on the phytoplankton community structure from one place to another or even at different times in the same place (Jones & Henderson 1987).

In the Gulf of Aqaba, both chlorophyll *a* concentrations and primary productivity have been concurrently studied by Levanon-Spanier et al. (1979). These authors presented an annual cycle of the two parameters during 1976–77 based on monthly measurements between the surface and 200 m in the north-western section of the gulf. Phytoplankton succession has been studied by Kimor & Golandsky (1977), and more recently by Lindell & Post (1995); these latter authors have also examined the pico-fraction. Studies that included chlorophyll *a* concentrations on the eastern coast of the Gulf of Aqaba were mostly restricted to coastal waters along the Jordanian coast or had temporal resolutions of 2–3 months (Leger & Artiges 1978, Natour & Nienhuis 1980, Mahasneh 1984, Wahbeh & Badran 1991, Badran & Foster 1998, Badran et al. 1999, Richter et al. 2001, Al-Najjar et al. 2003 Rasheed et al. 2003, and Niemann et al. 2004). Badran et al. (1999) and Rasheed et al. (2002) reported significantly higher nutrient and chlorophyll *a* concentrations in coastal coral reef waters as compared to the water column just 3 km offshore. Badran (2001) reported chlorophyll *a* and nutrient concentrations at a high temporal resolution for the eastern coast of the gulf down to 200 m and found relatively high concentrations during winter and low concentrations in the surface water during summer, when a subsurface maximum existed at about 75 m. Richter et al. (2001) have shown that coral reefs on the Jordanian side of the Gulf of Aqaba have a large internal regeneration surface dominated by encrusting filter feeders, mainly sponges, reaching 3–7 m^2 per projected m^2. Rasheed et al. (2003) have also shown rapid recycling in carbonate sediments associated with the coral reef. Most recently Niemann et al. (2004) showed that considerable amounts of coastal nutrients and primary production in the Gulf of Aqaba are driven offshore by cross-sectional density currents.

The main objective of the present study is to employ the ambient nitrate concentrations in a simple diffusion model to assess the nitrate flux across the summer thermocline and determine the f ratio 'fraction' of new to total primary production in waters of the Gulf of Aqaba during summer.

2. Material and methods

The study employs a simple mathematical model for the quantitative analysis of nitrate based on new primary production. Nitrate and

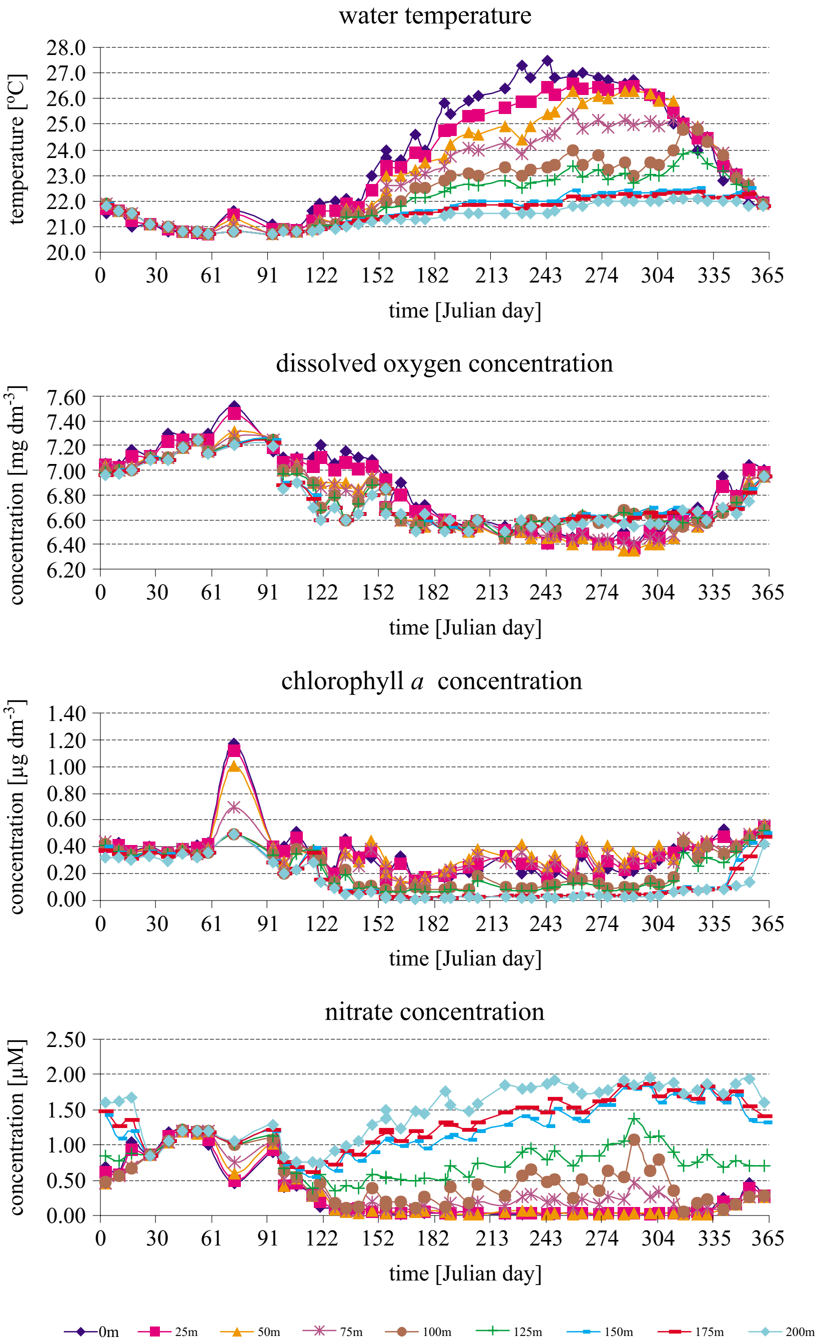

Fig. 1. Annual profiles of water temperature [°C], dissolved oxygen [mg dm^{-3}], chlorophyll *a* [μg dm^{-3}] and nitrate [μM] concentrations in the waters of the Gulf of Aqaba, Red Sea

chlorophyll a concentrations were measured on a regular basis between 1994 and 2000. Records were generated down to 200 m at a vertical resolution of 25 m – weekly during 1994 and 1995, and every two weeks from 1997 through to 2000. Inorganic nutrients – ammonium, nitrate, nitrite and phosphate – were analysed spectrophotometrically following well-established methods developed from Strickland & Parsons (1972). Chlorophyll a was measured fluorimetrically using the method of Arar & Collins (1992) after extraction in acetone (95%). Detailed nutrient and chlorophyll a results, mainly those collected during 1994–95, have been published by Badran (2001). Annual changes in salinity in the Gulf of Aqaba are insignificant (Manasrah et al. 2004). Temperature is therefore the main factor determining the density structure of the water column. Fig. 1 shows the annual profiles of water temperature, dissolved oxygen, chlorophyll a and nitrate concentrations over an annual cycle.

3. Simple diffusion model for the assessment of biological and physical stress factors k, K_z

The main focus of the study was to estimate the nitrate influx across the summer thermocline. For this purpose the seasonal course of the year was divided into two intervals: the summer stratification period (May – end of November; Julian day 120 to 335), when turbulent diffusion is the main driving force of vertical nutrient distribution across the thermocline and in the upper water, and the winter mixing period (Julian day 335 to 120), when the water constituents are homogeneously distributed throughout the mixed layer as a result of convective processes (Badran 2001). As Fig. 1 makes clear, a strong summer stratification exists between 50 m and 150 m. Therefore, the upper and lower boundaries of the summer thermocline were taken as 50 m and 150 m respectively. The model itself is a simple diffusion model originally developed by Garside (1985). Applying the model has two essential requirements: exponential fit of the summer nitrate concentration depth profile across the thermocline, and nitrogen limiting conditions. Fig. 2 shows the nitrate concentration distribution in the upper 200 m during summer and winter in the Gulf of Aqaba. The summer stratification nitrate distribution fulfils the exponential fit requirement across the thermocline extremely well ($R = 0.88$, $n = 450$, $p < 0.0001$). Fig. 3 shows the total inorganic nitrogen-phosphorus relationship, which provides strong evidence that the system is nitrogen-limited (see also Badran 2001).

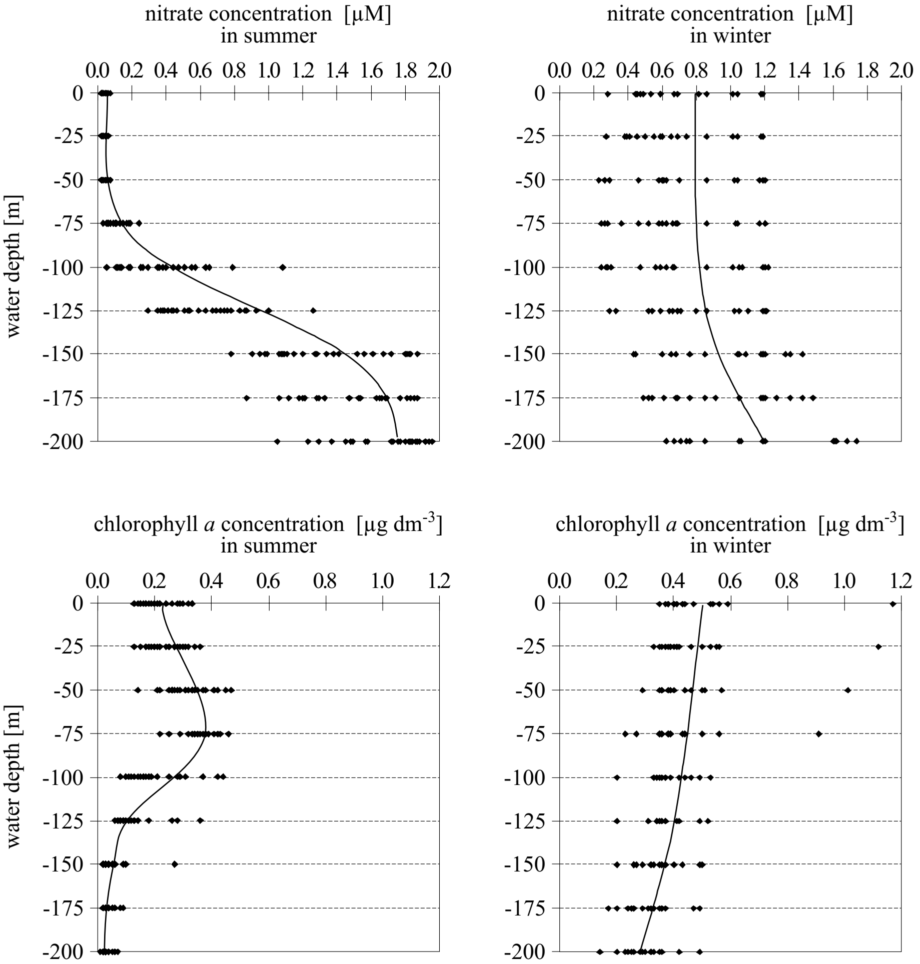

Fig. 2. Nitrate and chlorophyll *a* concentration profiles from the surface down to 200 m during summer stratification (left panel) and winter mixing (right panel) in the Gulf of Aqaba, Red Sea

Let F be the nitrate flux across the thermocline, K_z the eddy diffusivity, C the concentration and Z the water depth. Then,

$$F = K_z(dc/dZ). \tag{1}$$

If V is the phytoplankton uptake rate and k is an uptake rate constant, then assuming first-order kinetics for low concentrations,

$$V = kC. \tag{2}$$

Under steady-state, nitrogen-limiting conditions, we have

$$kC = dF/dZ = K_z(d^2C/dZ^2).$$

Rearranging this equation gives

$$d^2C/dZ^2 = kC/K_z.$$

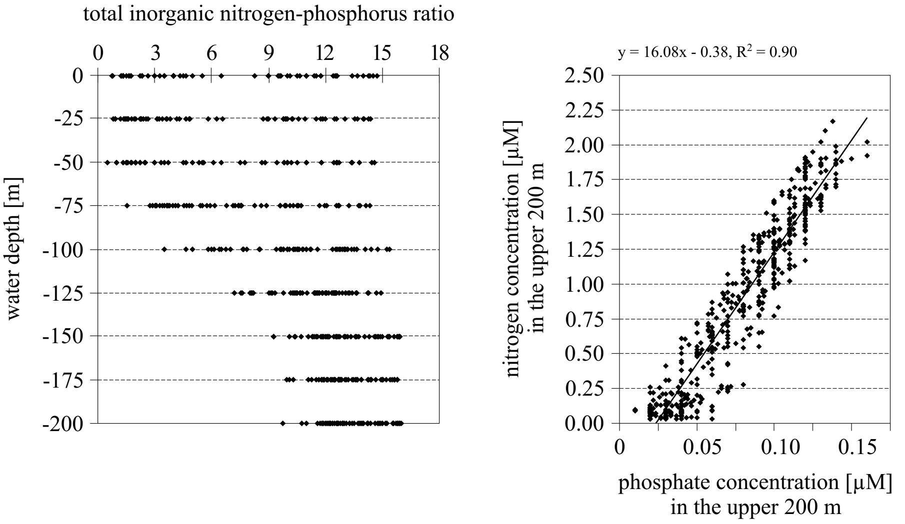

Fig. 3. Nitrogen versus phosphorus concentrations in the waters of the Gulf of Aqaba, Red Sea. Note the excess phosphorus at low concentrations indicating nitrogen limitation of phytoplankton production

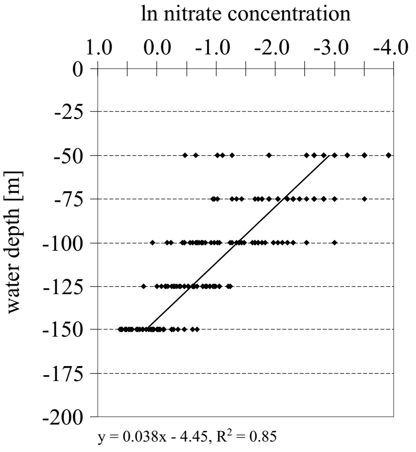

Fig. 4. Natural logarithm of nitrate concentrations versus depth across the summer thermocline in the Gulf of Aqaba, Red Sea. Note the linear relationship supporting the exponential fit. Depth Z in the regression equation is x and y is ln (C_z)

Solving the differential equation and taking natural logarithms yields

$$C_z = C_0 e^{z(k/K_z)1/2} ==> \ln C_z = \ln C_0 + Z(k/K_z)^{1/2}. \tag{3}$$

C_0 and C_z are the nitrate concentrations above the thermocline and at depth z respectively. Based on eq. (3), $(k/K_z)^{1/2}$ can be estimated from the slope of a plot of $\ln C$ versus depth across the thermocline (Fig. 4).

$$\text{Slope} = 0.038 = (k/K_z)^{1/2} ==> k/K_z = 1.44 \times 10^{-3}\ \text{m}^{-2}. \tag{4}$$

4. Results

4.1. Evaluation of K_z

Despite the large variability in K_z values in the literature, several authors still use them and employ generated data to evaluate k (Garside 1985). The present paper, however, uses the opposite approach. According to Denman & Gargett (1983) K_z values can span three orders of magnitude, between 10^{-3} and 10^{-6} m^2 s^{-1}. Values of k on the other hand are less variable but rarely found in the literature. But they can be calculated using the Michaelis-Menten equation. Uncertainty in k values is mainly due to the variable values of Michaelis-Menten equation constants. However, estimates of these constants are in the range of one order of magnitude only.

If $V_{\max}$ is the maximum uptake rate and K_m is the nitrogen concentration that can support half $V_{\max}$, then using the Michaelis-Menten equation,

$$V = V_{\max} C/(K_m + C). \tag{5}$$

From eqs. (2) and (5)

$$V_{\max} C/(K_m + C) = kC ==> k = V_{\max}/(K_m + C). \tag{6}$$

If $0.0 < C_{\mathrm{NO3}} < 0.1$ μM, then according to Dugdale (1967),

$$V_{\max} = 0.5 C_{\mathrm{NO3}} \text{ mmole m}^{-3} \text{ h}^{-1}. \tag{7}$$

Some K_m values in the literature are 2.5, 1.0, 0.5 μM (from Dugdale 1967, Fasham et al. 1990, Dugdale et al. 1995). Using a mean value gives

$$\text{Mean } K_m = 1.33 \ \mu\text{M}.$$

If we employ the mean value of C_{NO3} during the period May–November in the upper 50 m (0.035 μM), then from eq. (7) we obtain

$$V_{\max} = 0.50 \times 0.035 = 1.75 \times 10^{-2} \ \mu\text{M h}^{-1} =$$
$$= 4.86 \times 10^{-6} \text{ mmole m}^{-3} \text{ s}^{-1},$$

from eq. (6) we have

$$k = 0.0175/(1.33 + 0.035) = 1.28 \times 10^{-2} \text{ h}^{-1} = 3.56 \times 10^{-6} \text{ s}^{-1},$$

and from eq. (4) we get

$$K_z = 3.56 \times 10^{-6}/1.44 \times 10^{-3} = 2.47 \times 10^{-3} \text{ m}^2 \text{ s}^{-1}.$$

4.2. Estimation of the nitrogen flux

Nitrate flux in simple diffusion models is equal to the eddy diffusivity multiplied by the concentration gradient. In most studies the concentration gradient is calculated from the difference between the concentrations in the upper and the lower boundaries of the thermocline. This approach assumes a constant gradient across the thermocline, which is not necessarily true. A better approach is to divide the thermocline into smaller vertical intervals and calculate a mean concentration gradient across the thermocline using these smaller intervals. The greater the number of intervals and the smaller their length, the better is the estimated concentration gradient. In the present study, the summer thermocline was represented by the depth range 50–150 m. Measurements in this range covered four depth intervals. Mean concentration gradients in these four intervals during the period May –November are utilised for the nitrate flux estimation. Values of the estimated nitrate flux and all other related parameters are summarised in Table 1.

Table 1. Physical and biological state variables controlling the nitrogen flux across the summer thermocline in the northern sector of the Gulf of Aqaba

Variable	$V_{\max}$	K_m	k
value	4.86×10^{-6}	1.33	3.56×10^{-6}
units	mmole $m^{-3}\,s^{-1}$	mmole m^{-3}	s^{-1}
Variable	K_z	dC/dZ	F
value	2.47×10^{-3}	1.16×10^{-2}	2.82×10^{-5}
units	$m^2\,s^{-1}$	mmole m^{-4}	mmole $m^{-2}\,s^{-1}$

5. Discussion

5.1. New primary production *f* ratio 'fraction' during summer

Primary productivity during summer has been considered using both recent records generated through the Red Sea Program (1995–2000), and the old records of Levanon-Spanier et al. (1979). However, owing to differences in the measurement techniques, the recent records are believed to represent net primary productivity, while the old records were gross primary production (C. Haese, personal communication).

Nitrogen assimilation corresponds more to gross than to net primary production. Therefore, our calculations are based directly on the Levanon-Spanier et al. (1979) results. According to their Fig. 3, the mean value of 14 primary productivity measurements in the upper 100 m during the period May–August was 0.27 mg C m^{-3} h^{-1}. Integration over the euphotic zone (100 m) gives 27.0 mg C m^{-2} h^{-1}. Assuming 13 light hours per day gives an average daily primary production of 351 mg C m^{-2} d^{-1}. Taking this as a mean value for the summer (May–November; 215 days) primary productivity in the upper 100 m gives a total primary production for this period of 75.5 $\mathrm{g\,C\ m^{-2}}$. Converting this to nitrogen using Redfield ratios yields a consumption of 1.05 $\mathrm{mole\,N\ m^{-2}}$ (May–November)$^{-1}$. The amount of nitrogen that diffuses across the thermocline for this period calculated from Table 1 is 0.52 $\mathrm{mole\,N\ m^{-2}}$. This gives a mean f ratio, or better, fraction, of new to total primary production during summer of 0.50.

5.2. Comparison of the f fraction with values in other oligotrophic systems

Because of its direct relationship with carbon dioxide assimilation and the global carbon cycle, the question of nitrate-based, new primary production has been a serious long-term challenge in ocean chemistry. Estimates of the f fraction of new to total primary production vary by more than one order of magnitude. Some estimates at the lower limit of the range, however, are based on short-term observations and cannot account for the *in situ* changes in oxygen concentrations over an annual cycle (Lewis et al. 1986). Estimates of the f fraction based on long-term time-series analysis of oxygen data in the Sargasso Sea (Jenkins & Goldman 1985), on the diffusion of helium and tritium across the thermocline in the same area (Jenkins 1988) and on the exponential distribution of nitrate concentrations with depth in the northwest Atlantic (Garside 1985) were all around 0.50. The f value found in the present study is in good agreement with this.

High f ratio estimates encouraged Jenkins & Goldman (1985) to suggest that the ocean's capacity to absorb atmospheric carbon dioxide is underestimated and that there is a need to reassess global oceanic carbon budgets. However, before going that far, the reliability of high f value estimates needs to be discussed. In the present study, the f value gains reliability from the following factors: (i) the calculations are based on several years of actual records; (ii) the two estimated constants k and K_z used for the calculation of f are both within the accepted range in the literature (10^{-5}–10^{-6} $\mathrm{s^{-1}}$ and 10^{-3}–10^{-6} $\mathrm{m^2\ s^{-1}}$ respectively; Denman & Gargett 1983, Garside 1985, Lewis et al. 1986); (iii) the model employed has two major advantages over conventional diffusion models: it incorporates the k factor, which represents the biological stress resulting in diffusion, rather than considering the physical stress alone, and accounts for the statistically verified exponential distribution of nitrate down the water column rather than just assuming a simple linear fit without actual statistical testing; (iv) the annually fairly reproducible and seasonally limited variable atmospheric conditions of the Gulf of Aqaba make the assumption of a mean K_z value over summer not only suitable for the purpose of the present study but also applicable to the entire Gulf of Aqaba. In contrast, areas where dramatic atmospheric changes occur during summer require different K_z values for these different weather conditions. A good example is the Gulf of Aden, at the southern end of the Red Sea, where monsoons occur in mid-summer, resulting in strong upwelling (Alsayed & Gaddaf 1993, Böttger-Schnack 1995), which in turn results in much higher primary productivity (mainly new production) in the Gulf of Aden as compared to the Gulf of Aqaba.

5.3. Primary productivity during winter

In winter (December–April) the water column in the Gulf of Aqaba is well mixed. Such mixing conditions result in water properties being rapidly redistributed in the water column regardless of where they occur. The best examples are chlorophyll *a* and oxygen concentrations (Fig. 1), which acquire values at 200 m no different from the values in the surface water. The high chlorophyll *a* and dissolved oxygen concentrations below 100 m during winter cannot be the result of local primary production. They must have been produced in the euphotic zone and transported deeper on a time scale faster than that of both primary production and phytoplankton consumption/decomposition. This is supported by the fact that primary production below 100 m does not enhance chlorophyll *a* concentration during summer when the water is stratified; further, there is more surface irradiance, less shading, and the nutrient concentrations in the subsurface water are considerably higher. In winter mixing conditions, the question of new and regenerated primary productions becomes less important because, regardless of the rates of primary productivity, phytoplankton decomposition and zooplankton excretion, and the products of all processes are rapidly redistributed in the entire water column. Moreover, during winter, nitrogen is available in excess in the euphotic zone and does not limit primary productivity.

Atmospheric conditions, mainly irradiance, which varies considerably during winter owing to variability in the cloud cover, can be the main limiting factor of the winter primary production. Our records of winter chlorophyll *a* concentrations as well as those of Menzel & Ryther (1960) lend good support to this. The mean chlorophyll *a* concentration in the upper 100 m for a clear sky, calm sea, and fairly warm daytime seawater temperatures may exceed 1.00 μg dm^{-3}. Such a value was recorded in the present study in March. The records of Menzel & Ryther (1960) include a similar incident recorded in April, when primary productivity reached 20.0 mg C m^{-3} day^{-1}, the highest value ever reported anywhere according to these authors, and the maximum nitrogen-based potential production according to the estimates of the present study. These findings raise the question of the extent to which oligotrophic subtropical systems contribute to the assimilation of atmospheric carbon dioxide as compared to temperate systems, bearing in mind that primary productivity in subtropical systems is year-round while in temperate systems it is a summer-limited process.

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