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Community metabolism of a coral reef exposed to naturally varying dissolved inorganic nutrient loads

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Abstract Daily community rates of calcification, photosynthesis and respiration were measured on a coral reef located in the Northern Red Sea, Gulf of Eilat, Israel between March 2000 and March 2002. This reef is exposed to seasonally varying levels of inorganic nutrient loading due to mixing and stratification of the adjacent open sea water column. Net production measurements were positively and linearly correlated with open sea nutrient levels, and the community photosynthesis to respiration ratio varied between 0.9 and 1.7 accordingly. Community calcification varied between 30 ± 20 and 60 ± 20 mmol C m^{-2} day^{-1} during summer and winter, respectively. Under increased nutrient loading the relation between community calcification and aragonite saturation state is suppressed by 30% on average. Both of these findings demonstrate the deleterious effects of nutrient loading on coral reefs.

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Introduction

Many fringing and barrier coral reefs situated near densely populated regions around the world are exposed to varying degrees of anthropogenic dissolved and particulate nutrient loading caused by untreated sewage outflow, terrestrial runoff enriched in nutrients or mariculture (Smith et al. 1981; Hatcher et al. 1989; Bell 1992; Done 1992; Wachenfield 1998; Koop et al. 2001; Mosley and Aalbersberg 2003; Loya 2004; Silverman et al. 2004). In extreme cases of increased direct external nutrient supply to coral reefs, the fast growth of benthic macro-algae quickly smothers and displaces corals and other benthic invertebrates (Smith et al. 1981; Genin et al. 1995). However, in cases where nutrient sources are reduced and their supply to the coral reef is indirect, i.e. from geographically distant sources (Bell 1992; Lapointe et al. 2004), the relation between the observed shift in the benthic population structure of the reef towards autotrophic dominance and nutrient loading is still not well understood (Hughes 1994; Brown 1997; Lapointe 1997). This is because other environmental and ecological factors may be responsible for trophic shifts, such as disease outbreaks amongst corals (Loya 2004; Weil 2004) or sudden decline in grazing populations (Hughes 1994; Szamant 2002).

Occupation of hard substrate by benthic autotrophs also causes a decline in coral recruitment to the reef (Richmond 1997; Epstein et al. 1999). Without the ability to renew its coral population the benthic population of the reef will eventually shift towards autotrophic dominance. This change may be accompanied by higher grazing pressure and its associated bioerosion (e.g. Hallock 1988), thus upsetting the delicate balance between growth and erosion of the reef framework. Finally, laboratory and field experiments have shown that reef building corals reduce their rates of calcification, reproduction and resistance to disease in response to nutrient loading (e.g. Kinsey and Davies 1979; Ferrier-Pages et al. 2000; Harrison and Ward 2001; Koop et al. 2001; Bruno et al. 2003; Loya et al. 2004).

Calcification (G_{net}), photosynthesis (P_g) and respiration (R) are three major metabolic processes dominating the community metabolism of coral reef ecosystems (Hatcher 1997). By following changes in the dissolved oxygen (DO) and total alkalinity (A_T) of reef water, it is possible to evaluate the intensity of these processes at the community level (Marsh and Smith 1978; Smith 1978; Gattuso et al. 1999). In coral reef ecosystems, P_g and R are very high and almost equal. Hence, net production (P_n), which is the difference between the two, is often close to zero (e.g. Kinsey 1983, 1985; Pichon 1995, 1997). Similarly, the ratio P_g:R is close to unity indicating that the reef is in trophic balance. When P_g:R > 1, the reef is autotrophic and when P_g:R < 1 the reef is heterotrophic (Op. Cit.). Autotrophic reefs require an increased external supply of dissolved nutrients, while heterotrophic reefs require an increased supply of particulate organic matter (plankton; Marsh and Smith 1978; Erez 1990) and perhaps dissolved organic matter as well (Yahel et al. 2003) from the open sea to support its growth.

The trophic phase shifting expected in reefs exposed to increased nutrient loading should be reflected by an increase in the P_n (positive for DO and negative for C_T and nutrient budgets) and P_g:R > 1. The replacement of calcifying benthic heterotrophs by macro-algae and the physiological suppression of calcification should be reflected by an equivalent decrease in G_{net}.

The primary objective of this study is to verify the expected community scale metabolic response of a coral reef to low level dissolved inorganic nutrient loading described above. Measurements of community metabolic rates were made in the Nature Reserve coral Reef (NRR) located in the Northern Gulf of Aqaba, Israel. The NRR is exposed to naturally occurring seasonal fluctuations in the external supply of dissolved inorganic nutrients. These fluctuations result from surface cooling during the winter, which drives a vertical mixing of the water column and transports nutrient rich deep water to the surface, while during the summer, stratification decouples the surface layer from the deep water of the Gulf causing it to be severely depleted in nutrients (Reiss and Hottinger 1984; Genin et al. 1995).

The study site

The NRR is a fringing reef situated along the Western shore of the Gulf, approximately 10 km south of the city of Eilat (Fig. 1). See Loya and Solodkin (1971) as opposed to Loya (2004) for in depth descriptions of the reef morphology and changes in its community structure over the past three decades. During this period the NRR has undergone severe deterioration resulting from extreme low tides, oil spills, sewage pollution, phosphate dust loading and intense diving pressure (Epstein et al. 1999; Zakai and Chadwick-Furman 2002; Loya 2004). During the last two decades some anthropogenic stress factors have been reduced significantly. The oil port reduced its activity significantly since 1983, and the municipal sewage of Aqaba and Eilat were diverted to oxidation treatment systems in 1986 and 1996, respectively. However, in the last 8 years the massive development of fish farming in cages at the northern end of the Gulf has introduced a substantial new source of nutrients to Gulf water (Lazar and Erez 2004). This addition significantly augmented the naturally occurring seasonal fluctuations in open water nutrient levels. In the late 1990's the reef had

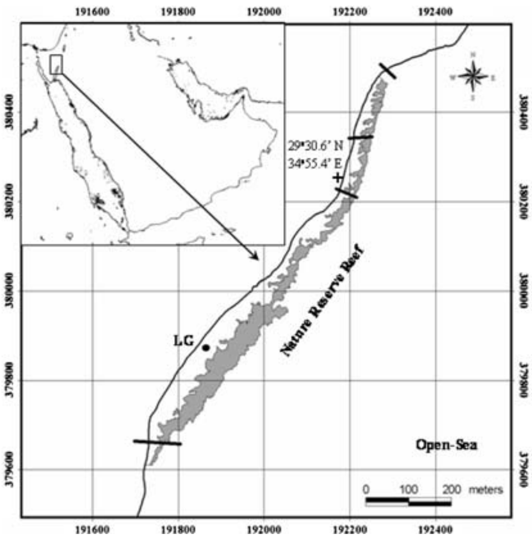


Fig. 1 (**a**) The Gulf of Aqaba is connected to the Northern Red Sea through the Strait of Tiran, which is a shallow sill (250 m). Therefore, only warm, nutrient-poor surface water enters from the Red Sea. The arid conditions prevailing in this region provide virtually no nutrient input from ground runoff. As a result the Gulf is considered to be highly oligotrophic providing ideal conditions for coral reef development at relatively high latitude. (**b**) The NRR is a fringing reef approximately 1 km long on the Western shore of the Gulf, 10 km south of the town of Eilat. The grey outlined area marks the reef flat. The lagoon is narrow (20–50 m) and the fore-reef extends to a depth of 40 m some 50–70 m to seaward from the reef flat. The black lines indicate foot bridges and jetties crossing over the reef. The sampling site in the lagoon (LG) is indicated by a black dot approximately 200 m north of the southern boundary (the map was created at the Israeli National Parks and Nature Authority's GIS unit)

lost ca. 50–60% of its live coral cover relative to values reported for the late 1980's in the 4–12 m depth range (Zakai 2000; Loya 2004). It has been suggested that this reduction may have been caused by the nearby fish farming activities (Loya 2004). Furthermore, coral recruitment has decreased by 53–96% during the same period (Zakai 2000). During the study period (2000–2002) the coral live cover was only 20–40% according to several authors (Zakai 2000; Loya 2004; Genin and Silverman 2004).

The net surface flow along the western coast of the Gulf of Aqaba at its northern tip is southward during most of the year except for a short period of northward flow between November and January (Genin and Paldor 1998). Near the reef the current velocity varies between 0 and 10 cm s^{-1} and has an on-shore component of 0–2 cm s^{-1}. Both on-shore and long-shore components are modified by the wind and tide. The generally southern current is driven by the prevailing northerly wind, blowing from this direction ca. 90% of the time (Op. Cit.). This current is weaker during the flood period of the tide in comparison to the ebb period of the tide. The wind is usually strongest during the daytime hours reaching velocities of up to 10 m s^{-1} along the longitudinal axis of the Gulf, which possibly increases the magnitude of the on-shore component of the current.

The chemical constituents of water flowing in this fashion over the reef into the lagoon are modified by photosynthesis, respiration and calcification (Korpal 1991; Barnes and Lazar 1993; Silverman et al. 2004, 2005). However, their values also reflect the rate of water exchange between the reef and the open sea. This rate can be assessed by following changes in a conservative parameter such as salinity. The cyclic behavior of salinity in the reef compared to its relatively constant value in the adjacent open sea is shown in Fig. 2. This behavior reflects the effects of

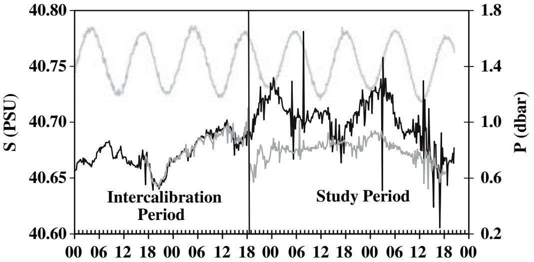


Fig. 2 Salinity at NRR lagoon (heavy black line) and fore-reef (heavy grey line) compared to water pressure in the lagoon (speckled black line) during 25–28/5/2003. The data loggers were deployed together initially for 24 h in the NRR lagoon after which one of them was removed to the fore reef to a depth of 3 m for the rest of the study. Note that during low tide the salinity in the lagoon increases while at high tide it becomes similar to that of the fore-reef. However, the daily average salinity anomaly is positive due to evaporation indicating that flushing of reef water with relatively fresh open sea water is not instantaneous and that residence time is finite and on the order of hours. The relatively constant salinity in the fore-reef is considered to represent that of the open sea and was used to calculate the residence time of water in the reef (Eq. 1)

evaporation and the flushing of the reef with relatively fresher water from the open sea and can be used to assess the residence time (τ) of water in the reef. Furthermore, such behavior supports the assumption that measurements of the relevant chemical constituents made in the lagoon indeed represent the cumulative effects of biological processes taking place between the fore-reef and the shore.

Materials and methods

Community metabolism studies were conducted at the NRR throughout the period 3/2000–3/2002 at 1–2 month intervals. Metabolic rates were assessed using data gathered from diurnal cycle measurements at a single station in the reef (LG in Fig. 1). Samples of water were taken in 5 l GOFLO Niskin bottles from the reef at LG every 3–4 h over a total period of 36–48 h, as well as 2–4 samples from the open sea water approximately 0.5–1 km offshore. These samples were analyzed for: DO, pH, A_T, nutrients (NO_2^{-1}, NO_3^{-2}), Chlorophyll *a*, and salinity. Automated measurements of temperature, salinity, pressure, pH and DO were recorded at 10 min intervals by a SBE-16 data logger deployed at LG. In a few of the field studies current direction and speed were measured with an inter-ocean ltd. S4 current meter deployed on the reef-flat near LG.

DO was measured using the modified Winkler method (Strickland and Parsons 1972) with a Metrohm auto burette (precision of ± 1 µmol l^{-1}). pH samples were refrigerated and measured at the end of the sampling cycle using a Radiometer PHM93 combined glass electrode calibrated with Radiometer commercial buffers at 25°C. Samples were warmed at room temperature initially and prior to measurement were kept and measured in a temperature controlled bath at 25 ± 0.1°C (precision of ±0.001–0.003 pH units). A_T samples were refrigerated and measured at the end of the sampling cycle after filtering approximately 15 g of the sample per replicate into a tephlon cup through a 0.45 µm Sartorius filter. Samples were then titrated in an open cell with 0.015 N HCl using an automated Metler Toledo DL-67 titrameter to below the inflexion point and down to pH = 3. A_T values were calculated according to the method outlined by Sass and Ben-Yaakov (1977) and had a precision of better than ± 2 μeq kg^{-1}. The accuracy of these measurements was confirmed with a certified reference standard from A. Dickson's laboratory. Chlorophyll *a* was measured using the fluoremetric method outlined in Parsons et al. (1985), using a Turner AU10 fluorometer. Salinity was measured with an AGE-2100 salinometer calibrated with IAPSO standard seawater (SD = ± 0.003 PSU). Nitrite (NO_2^{-1}) was measured with a colorimetric method described by Grassohoff et al. (1999) using a Flow Injection Autoanalyzer (Lachat Instruments Model QuickChem 8000). Nitrate (NO_3^{-1}) was measured by reducing it to nitrite using a copperized cadmium column (precision of nitrite and nitrate measurements was ± 0.02 µmol l^{-1}).

A_T and pH measurements were used to calculate the carbonate system in seawater together with the apparent thermodynamic ion activity scale constants (NBS) calculated from salinity and temperature according to Mehrbach et al. (1973). Residence times of water in the reef (τ = reef water volume/water transport over the reef flat) were estimated using a salt and water budget according to Smith (1978). The 24 h average as opposed to the momentary salinity in the reef ($S_{\text{reef-24}}$) was assumed to be at steady state relative to the open sea ($S_{\text{open-sea}}$, Fig. 2, Eq. 1) throughout the duration of the study. Evaporation (E) was calculated according to a simplified version of Fairall et al. (1996) TOGA/COARE code using the hfbulktc.m matlab function in the airsea toolbox (ver. 2.0, 1999), developed by R. Pawlowicz and A. Anis (available for download at http://www.eos.ubc.ca/about/faculty/R.Pawlowicz.html). Wind speed, dry and wet bulb air temperature, and air pressure, required for this function were measured at the Interuniversity Institute (IUI) jetty about 400 m south of LG along the coast at 10 min intervals.

Average daily rates of P_n and G_{net} were estimated per horizontal unit area of the reef as a function of the difference between the diurnal average DO and specific A_T (A_T normalized for changes in LG salinity relative to open sea) respectively from their corresponding open sea values and the rate of water exchange between them (Eqs. 2 and 3). The difference in A_T is multiplied by a factor of 0.5 (Eq. 3) in order to convert the rate to mols carbon per m^2 per day units. Community respiration (R) was assumed to be constant over the 24 h period (Marsh and Smith 1978) and was calculated from the maximum night time depletion of reef DO relative to open sea DO, daily average depth (Z) and τ (hence R_{max}, Eq. 4). Estimates of P_n and R_{max} also take into account the exchange of oxygen between reef water and the atmosphere. This flux is calculated as the product of the difference between reef water DO and its saturation value (according to Weiss 1970) and the piston velocity (k, according to Waninkhof 1992). Daily and nighttime average wind velocities were used to compute daily (k_{24}) and nighttime (k_{night}) average piston velocities, respectively. Community gross production (P_g) was calculated from the difference between P_n and R ($R = 24 \cdot R_{max}$). Error evaluations in the calculated residence times and metabolic rates were made with the analytical errors of each input parameter and the first differential method (Topping 1972).

$$\tau = \frac{Z}{E} \cdot \frac{\left(S_{reef} - S_{open-sea}\right)}{S_{open-sea}} \tag{1}$$

$$P_n = \frac{Z}{\tau} \cdot \left(DO_{reef-24} - DO_{open-sea}\right) - k_{24} \cdot \left(DO_{sat(T,S)} - DO_{reef-24}\right) \tag{2}$$

$$G = \frac{Z}{\tau} \cdot \left(A_{T_{open-sea}} - A_{T_{reef-24}}\right) \cdot \frac{1}{2} \tag{3}$$

$$R_{max} = \frac{Z}{\tau} \cdot \left(DO_{open-sea} - DO_{reef-min}\right) + k_{night} \cdot \left(DO_{sat(T,S)} - DO_{reef} - min\right) \tag{4}$$

Results

Open sea nitrate (NO_3^{-1}) levels reached 1.5 µmol l^{-1} in March 2000, 1.4 µmol l^{-1} at the end of February 2001 and 0.7 µmol l^{-1} in January 2002 (Fig. 3, Table 1). In the summers of 2000 and 2001 open sea water column stratification caused severe depletion in NO_3^{-1} (~0.05 µmol l^{-1}) in the surface layer. Variations in chlorophyll *a* reflect the abundance of nutrients available for primary production and stayed at ca. 0.1 µg l^{-1} throughout the summers and rose as high as ca. 0.8 µg l^{-1} during the winters.

Diurnal cycles of DO, specific A_T and pH in the NRR lagoon are presented relative to their corresponding open sea values for two studies

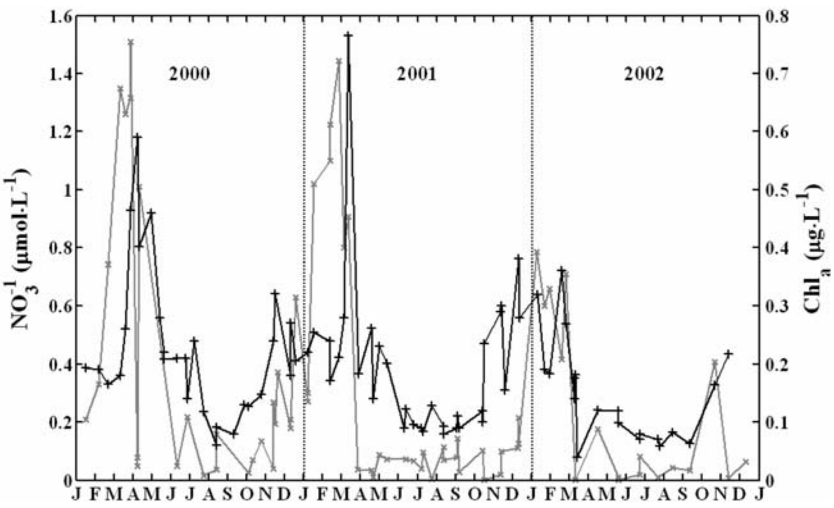


Fig. 3 Annual cycle of nitrate (NO_3^{-1}) (grey line with x markers), and chlorophyll *a* (black line with + markers) concentrations in the open sea seawater 0.5–5 km offshore from the NRR measured between January 2000 and December 2002

Table 1 Summary of measurements made at the NRR lagoon station and the adjacent Open Sea (OS)

Date	Mar-00	Oct-00	Nov-00	Dec-00	Jan-01	Feb-01	Mar-01	May-01	Jun-01	Jul-01	Sep-01	Oct-01	Dec-01	Jan-02	Mar-02
T_{avg} (°C)	20.56	25.14	22.47	21.86	21.22	20.87	21.94	22.97	23.77	27.24	26.48	25.38	22.26	21.15	21.27
GR^{a}_{avg} (watt m^{-2})	259	217	137	132	148	228	283	292	325	315	279	193	151	147	221
S^{b}_{avg} (PSU)	40.74	40.76	40.83	40.77	40.81	40.82	40.66	40.61	40.56	40.69	40.76	40.88	40.74	40.73	40.6
S^{c}_{os} (PSU)	40.72	40.72	40.79	40.73	40.78	40.78	40.63	40.58	40.53	40.66	40.72	40.84	40.7	40.69	40.58
Z^{d} (m)	1.7	1.5	1.7	1.7	1.8	1.7	1.7	1.7	1.6	1.5	1.5	1.6	1.7	1.7	1.8
E^{e} (mm day^{-1})	4	7	7.3	8	7	7.5	5	4.7	5	5.5	7.2	7	8	7	6
k^{f}_{night} (m h^{-1})	0.05	0.04	0.02	0.02	0.02	0.03	0.01	0.01	0.02	0.02	0.01	0.02	0.02	0.02	0.02
k^{f}_{24} (m h^{-1})	1.67	1.09	0.89	0.80	0.71	0.94	0.33	0.33	1.09	1.09	0.35	0.75	0.63	0.89	0.63
τ_{24} (h)	5	5.1	4.8	5	4.5	5.3	6	6.4	4.7	4.8	4.9	4.8	5.5	5.9	3.6
DO_{avg} (μmol l^{-1})	227	206	216	218	222	231	218	219	213	200	209	211	214	217	225
DO_{min} (μmol l^{-1})	197	163	193	199	194	191	170	190	162	150	167	175	197	203	191
DO_{max} (μmol l^{-1})	282	262	247	250	268	310	289	256	258	248	267	256	242	241	259
DO_{OS} (μmol l^{-1})	217	210	213	212	215	217	226	220	219	207	207	211	212	214	223
pH_{avg}	8.243	8.188	8.184	8.184	8.260	8.218	8.195	8.175	8.175	8.202	8.217	8.212	8.180	8.192	8.204
pH_{min}	8.202	8.137	8.143	8.152	8.226	8.157	8.138	8.136	8.083	8.127	8.162	8.160	8.153	8.170	8.152
pH_{max}	8.345	8.256	8.229	8.226	8.306	8.337	8.273	8.211	8.262	8.281	8.294	8.289	8.218	8.229	8.251
pH_{OS}	8.242	8.213	8.176	8.181	8.263	8.204	8.226	8.183	8.182	8.213	8.218	8.214	8.192	8.194	8.205
$A_{T\ avg}$ (μeq kg^{-1})	2487	2475	2480	2479	2480	2480	2479	2480	2481	2468	2475	2477	2476	2490	2478
$A_{T\ min}$ (μeq kg^{-1})	2467	2451	2472	2471	2469	2452	2455	2466	2456	2448	2446	2493	2463	2484	2470
$A_{T\ max}$ (μeq kg^{-1})	2500	2489	2485	2486	2490	2493	2489	2494	2495	2487	2492	2455	2486	2494	2489
$A_{T\ OS}$ (μeq kg^{-1})	2492	2490	2488	2486	2491	2491	2493	2490	2492	2487	2493	2493	2487	2489	2486
$NO_3^{-1}{}_{OS}$ (μmol l^{-1})	1.51	0.02	0.37	0.63	1.02	1.44	0.04	0.09	0.07	0.01	0.03	0.01	0.22	0.78	0.01

Daily average values of DO, pH and specific A_T are the 24 h sum of trapezoids throughout the entire measurement period of each study (36–48 h)

[a] Average of the 144 point moving average of Global Radiation (GR, 10 min interval) at IUI jetty mast for the 48 h of each study

[b] Average of the 144 point moving average of CTD conductivity measurements at NRR lagoon average for the 48 h of each study

[c] Minimum CTD conductivity during the diurnal cycle (see Fig. 3)

[d] Estimated 24 h average depth of the whole reef using the 24 h average CTD pressure measurement and the height of the CTD above the whole reef datum ($Z = Z_{24\text{–}avg} + 0.36$ m). The datum was established by conducting a detailed bathymetric survey of the lagoon and reef flat

[e] Rate of evaporation was estimated from the 24 h average latent heat flux (see above in methods section) using meteorological data from the IUI pier

[f] Values of nighttime (sun set to sun rise) and daily average piston velocities (k_{night} and k_{24}) calculated according to Wanninkhof (1992) with the average values of S and T measured in the NRR lagoon, and wind speed measured at the IUI

conducted during 25–26/2/2001 and 23–25/7/2001 (Fig. 4a–j). These cycles display the characteristic behavior of the measured parameters during winter and summer respectively. The diurnal extremes and daily average values for these parameters for all studies are presented in Table 1. DO in the reef (Fig. 4a, b) rises from a minimum value at the end of the night, which is lower than its open sea value. Initially, flushing of the reef with open sea water and atmospheric exchange increase DO, which is well bellow saturation. After daybreak excess photosynthesis over respiration raises reef DO above its open sea concentration. A maximum value is obtained in the early to late afternoon after which DO begins to decrease monotonically in response to excess community respiration, flushing of the reef with lower DO water from the open sea as well as degassing of excess oxygen, which is above saturation, to the atmosphere. During the winter the daytime DO differences from the open sea were usually higher than nighttime differences indicating that the reef was a net producer. However, during the summer the daytime differences were approximately the same if not lower than the nighttime, indicating that the reef was operating in trophic or slightly heterotrophic balance.

Specific A_T (Fig. 4c, d) in the reef in the early morning hours is similar to the open sea value, indicating that either G_{net} is equal to the alkalinity flux from the open sea or that net calcification is 0. Throughout the morning and early to late afternoon specific A_T decreases monotonically to a minimum value relative to its constant value in the open sea in response to net calcification. Note the apparent correlation between the daytime DO and A_T signal, which reflects the previously reported light enhanced calcification (e.g. Barnes and Chalker 1990). From late afternoon to midnight specific A_T increases to near open sea values and remains so until morning. Nighttime

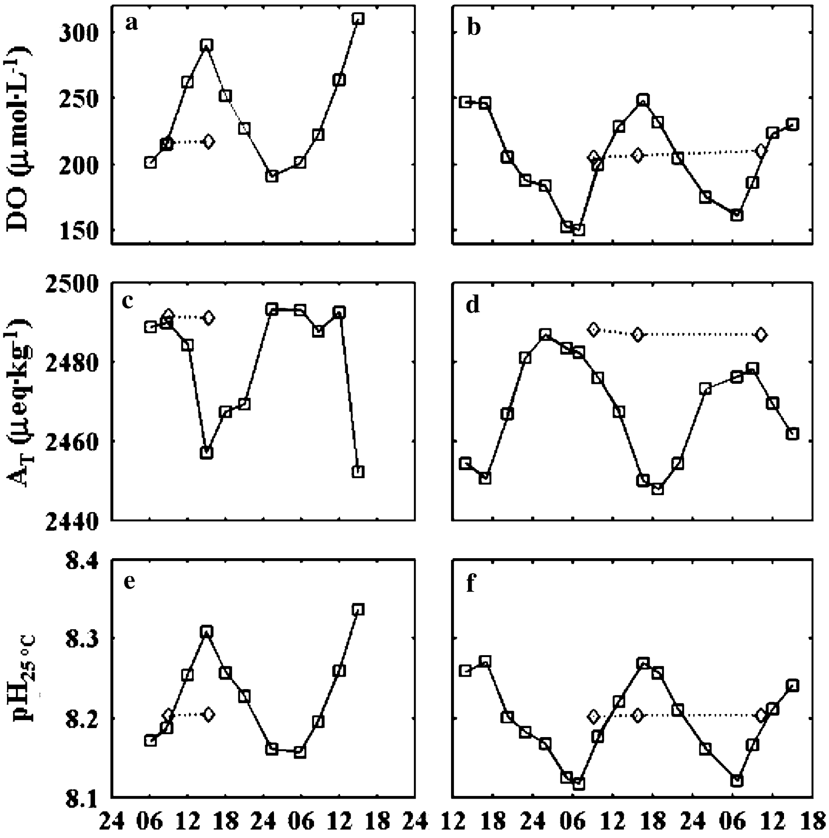


Fig. 4 Diurnal cycles of Dissolved Oxygen (DO), specific Total Alkalinity (A_T) and pH (NBS at 25°C) in the NRR lagoon (empty squares) and open sea (empty diamonds), during 2/2001 (**a**, **c**, **e**) and 7/2001 (**b**, **d**, **f**)

values were usually slightly lower (ΔA-$_{T < 5\ \mu eq\ kg}$$^{-1}$) than open sea, however in some of the winter studies such as Mar 2000 and Jan 2002 the reef specific A_T rose well above open sea indicating net dissolution of $CaCO_3$. Remineralization of organic matter (NH_4^+ production) during the nighttime is responsible for a small fraction of the increase in specific A_T throughout the night (ca. 3%, data not shown).

The diurnal cycle of pH (Fig. 4e, f) reflects the combined effects of photosynthesis, respiration, calcification in the reef and water exchange with the open sea. The uptake of C_T associated with photosynthesis (increasing DO) causes pH to increase, and decrease in response to respiration, which increases C_T (decreasing DO). The uptake or evolution of C_T associated with $CaCO_3$ deposition or dissolution result in a decrease or increase in pH in accordance with a decrease or increase in A_T, respectively. Thus, during the daytime pH rose from a minimum at day break, which was well below its open sea value, to a maximum value in the early to late afternoon, which was well above its open sea value. The decrease in pH occurred in step with the decrease in DO in response to excess respiration over photosynthesis and water exchange with the open sea. The continuing decrease below open sea values throughout the night is due to respiration considering that the difference in reef A_T relative to open sea is very small (very little calcification). Although the diurnal cycle of pH and DO are very similar, comparison of the pH and DO daytime and nighttime departures from their corresponding open sea values in all studies indicates that daytime calcification can be detected in the pH signal (Fig. 5). Note that the nighttime intercept is very close to 0, indicating that pH and DO are exclusively interdependent and reflect the evolution of C_T (consumption of DO) in the reef in response to community respiration. The daytime increase in calcification, which reduces pH but not DO, is reflected by the lower slope of the ΔDO:ΔpH trend line.

The daily average metabolic rates presented in Table 2 were calculated with the data presented in Table 1 and Eqs. 1–4. Also included are rates from earlier studies conducted during June 1997, February and September 1998. Although P_n, P_g and R were assessed from DO measurements they are presented in carbon units. This conversion takes into account a ratio between the change in dissolved oxygen and dissolved inorganic carbon as a result of photosynthesis and respiration of 1. This quotient was assessed for the NRR in an earlier study conducted by Barnes and Lazar (1993) and was verified in the 1997/98 studies, during which water samples were analyzed for C_T as well.

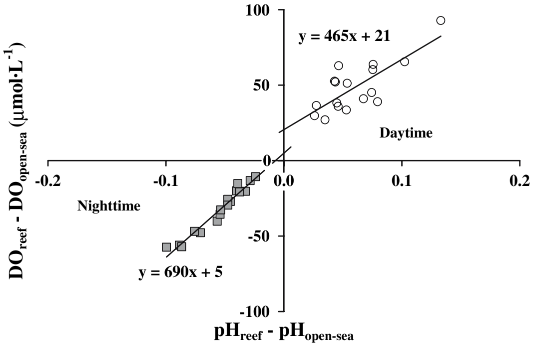


Fig. 5 Comparison of the daytime (empty circles) and nighttime (grey squares) departures of DO and pH (measured at 25°C) from their corresponding open-sea values at NRR for studies between 3/2000–2002

During the winter (November–March), average G_{net} is 30 ± 20 mmol C m^{-2} day^{-1} and P_g:R is 1.4 ± 0.3, while during the summer, average G_{net} is 60 ± 20 mmol C m^{-2} day^{-1} and P_g:R is 1.0 ± 0.1 (Table 3). P_g:R and G_{net} vary considerably between 0.9–1.9 and –4–70 mmol C m^{-2} day^{-1} respectively during the period 3/2000–3/2002 and appear to fluctuate seasonally in opposite phase (Table 2, Fig. 6). A similar seasonal pattern is apparent in earlier studies conducted at the NRR, during June 1997 (summer), February 1998 (winter) and September 1998 (summer). G_{net} varies between 40 and 110 mmol C m^{-2} day^{-1} independently of P_g:R, which is ~1 (including late 1990's studies), while for higher P_g:R, G_{net} is on average lower and relatively constant (Fig. 7c). As expected P_g:R is well correlated with open sea NO_3^{-1} levels (Fig. 7a, n = 17, R^2 = 0.82). However, open sea nutrient levels covary with temperature below 23°C (except Mar 2001 and 2002) suggesting that the increase in P_g:R may be caused by respiration decrease with temperature. In fact, there is a very week negative correlation between R and

Table 2 Community metabolic rates (calculated with input data from Table 1 according to Eqs. 2–4) and ratios for the NRR measured between 1997 and 2002

Date	P_g*	R*	P_n*	P_g:R	G_{net}*
6/1997	716 ± 34	705 ± 14	11 ± 20	1.0 ± 0.1	91 ± 15
2/1998	382 ± 27	268 ± 12	114 ± 16	1.4 ± 0.1	37 ± 10
9/1998	494 ± 27	399 ± 12	95 ± 16	1.2 ± 0.1	108 ± 10
3/2000	323 ± 25	199 ± 12	124 ± 13	1.6 ± 0.1	17 ± 9
10/2000	393 ± 27	372 ± 13	21 ± 14	1.1 ± 0.1	54 ± 7
11/2000	208 ± 31	183 ± 14	25 ± 17	1.1 ± 0.1	35 ± 9
12/2000	170 ± 31	117 ± 15	53 ± 16	1.5 ± 0.1	31 ± 9
1/2001	341 ± 29	248 ± 12	94 ± 16	1.4 ± 0.1	54 ± 11
2/2001	382 ± 26	201 ± 13	180 ± 13	1.9 ± 0.1	53 ± 11
3/2001	354 ± 27	372 ± 14	–18 ± 14	0.9 ± 0.1	49 ± 7
5/2001	172 ± 26	179 ± 14	–7 ± 13	1.0 ± 0.1	32 ± 6
6/2001	430 ± 26	464 ± 11	–34 ± 15	0.9 ± 0.1	38 ± 8
7/2001	393 ± 27	432 ± 11	–39 ± 15	0.9 ± 0.1	70 ± 8
9/2001	323 ± 28	303 ± 13	21 ± 15	1.1 ± 0.1	66 ± 8
10/2001	317 ± 28	308 ± 12	9 ± 16	1.0 ± 0.1	65 ± 9
12/2001	188 ± 29	161 ± 14	27 ± 15	1.2 ± 0.1	40 ± 8
1/2002	85 ± 28	103 ± 14	18 ± 14	1.2 ± 0.1	–4 ± 7
3/2002	427 ± 26	411 ± 2	17 ± 23	1.0 ± 0.1	49 ± 15

*Rates and errors are presented in units of mmol C m^{-2} day^{-1}

temperature ($n = 17$, $R^2 = 0.29$). Furthermore, net production estimated from the diurnal reef NO_3^{-1} cycle ($P_{n\text{-}N}$) decreases with open sea NO_3^{-1} (Fig. 7b), i.e. increased open sea NO_3^{-1} uptake by the reef, which also supports the apparent relation of P_g:R with NO_3^{-1}.

G_{net} varies between 30 and 110 mmol C m^{-2} day^{-1} (including the 1997/8 values) at low NO_3^{-1} (near 0) and is relatively low and constant (30–55 mmol C m^{-2} day^{-1}) for higher NO_3^{-1} levels (Fig. 7d). In contrast G_{net} is positively correlated with the reef's diurnal average temperature (Fig. 8a). Sorting the data according to their contemporaneous open sea NO_3^{-1} above and below 0.2 μmol l^{-1}, indicates that G_{net} is positively related to temperature above 23°C. Without the data points for Mar 2000 and Jan 2002 (grey squares in Fig. 8a), both high and low NO_3^{-1} (Mar 2001/02) data points appear to be negatively correlated with temperature below 23°C. The annual cycle of G_{net} with temperature and periodic averages of P_g:R and pH are indicated by the dashed line and text in Fig. 8b. According to this plot G_{net} decreases with decreasing temperature while P_g:R and diurnal average pH stay relatively constant at 1 and 8.193–8.197 (pH is corrected for in situ diurnal average temperature), respectively from May to October. During the period

Table 3 Metbolic performance summary for the NRR during March 2000–2002 together with average values measured on other Red-Sea reefs (Silverman et al. 2004) and Indo-Pacific reefs (Kinsey 1985; Pichon 1997)

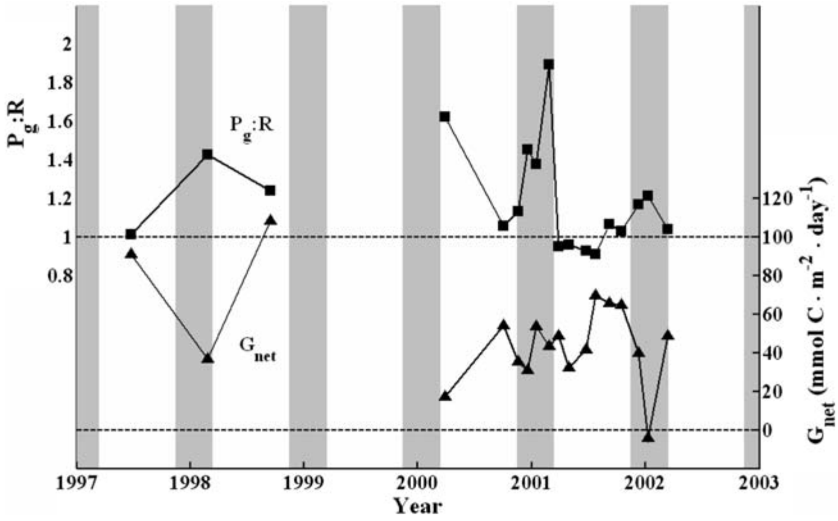
	P_g *	R*	P_n*	P_g:R	G_{net}*
Annual average	340 ± 140	300 ± 150	40 ± 150	1.2 ± 0.3	50 ± 25
Summer average	400 ± 140	390 ± 140	8 ± 38	1.0 ± 0.1	60 ± 20
Winter average	260 ± 110	180 ± 60	80 ± 60	1.4 ± 0.3	30 ± 20
Red-Sea reefs[a]	640 ± 240	970 ± 530	–320 ± 330	0.7 ± 0.2	210 ± 50
Kinsey (1985)	580 ± 50	580 ± 50	0	1 ± 0.1	110 ± 20
Pichon (1997)[b]	740 ± 440	570 ± 340	170 ± 240	1.3 ± 0.4	130 ± 90

*Rates and deviations are presented in units of mmol C m^{-2} day^{-1}

[a] Averages of metabolic rate measured at Ras Abu-Galum (Sinai Peninsula), Bullisar Island (Dahlak Archipelago) and NRR in the early 1990's

[b] Averages of all the values presented in Pichon (1997) and their standard deviation

Fig. 6 Seasonal variations in P_g:R (filled squares) and G_{net} (filled triangles) at NRR between 1997 and 2002. Shaded areas represent the winter of each year (mid November to mid March) with respect to water column structure and open sea NO_3^{-1} levels (Fig. 3)



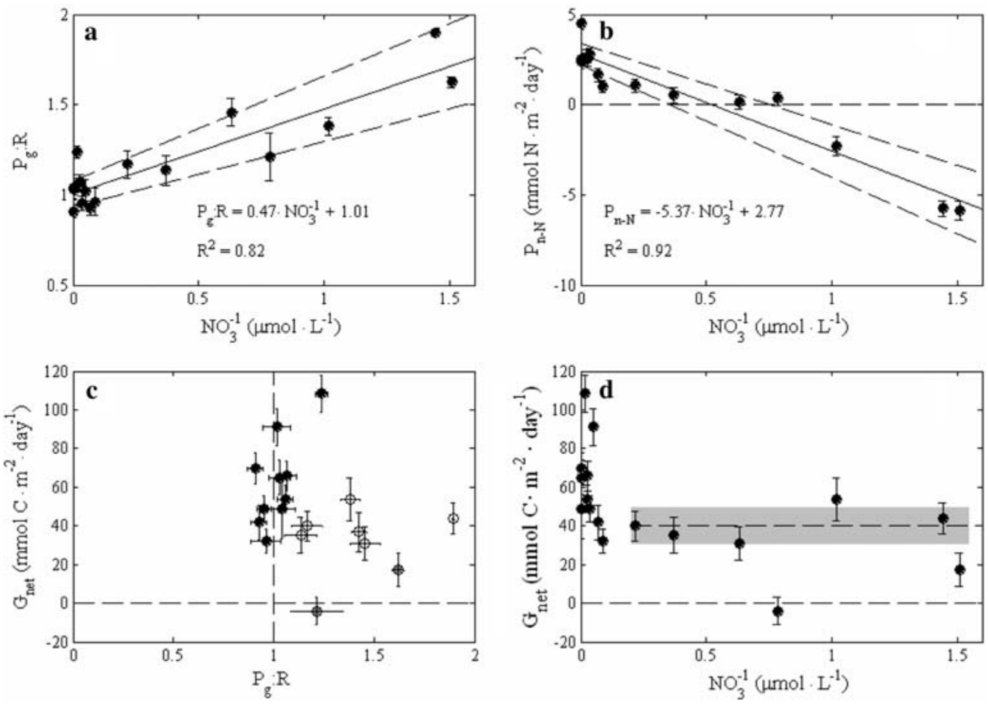


Fig. 7 (**a**) P_g:R versus open-sea concentration of NO_3^{-1} for all studies conducted at NRR during 2000–2002. The black line indicates the calculated linear trend and the dashed lines indicate the boundaries of the 95% confidence interval. (**b**) Net production estimated from the diurnal cycle of NO_3^{-1} ($P_{n\text{-}N}$) in the NRR plotted against the open sea NO_3^{-1} concentration for all studies conducted between 2000–2002. The black line indicates the calculated linear trend and the dashed lines indicate the boundaries of the 95% confidence interval. (**c**) Community calcification rate (G_{net}) plotted against P_g:R at NRR for all studies conducted during 2000–2002. Black filled and empty circles indicate data points with open sea $NO_3^{-1} < 0.2$ and > 0.2 μmol l^{-1}, respectively. Grey filled circles indicate the 3/2000 and 1/2002 studies for which extreme weather conditions occurred. (**d**) G_{net} plotted versus open sea NO_3^{-1} at NRR measured during the period 2000–2002. The grey shaded area includes studies where the open sea NO_3^{-1} concentration was greater than 0.2 μmol l^{-1} indicating that during the winter G_{net} is lower than summer and relatively constant

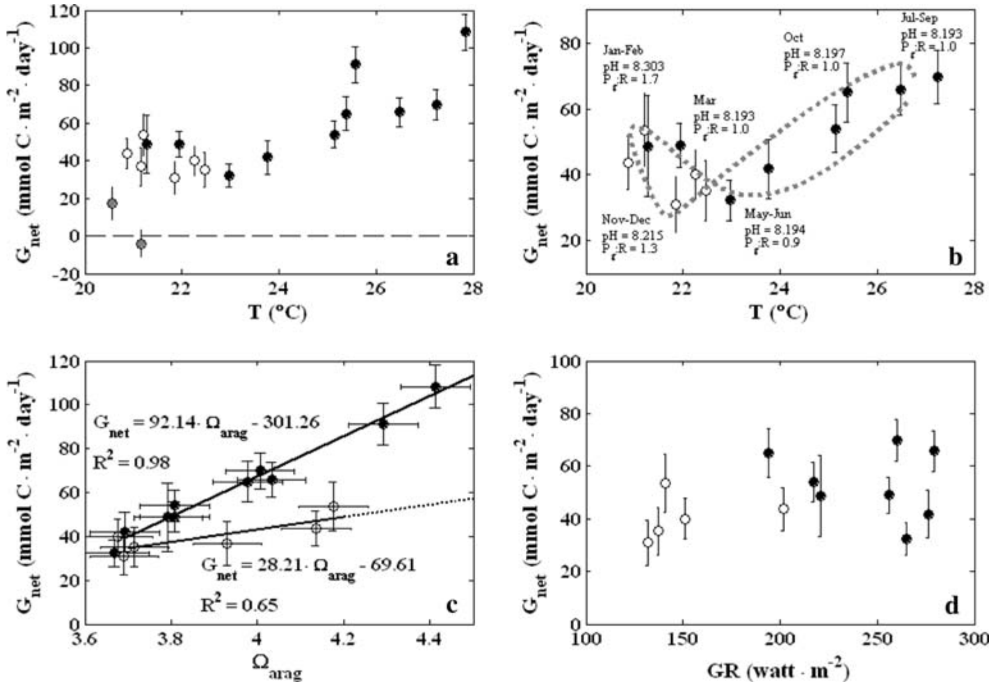


Fig. 8 (**a**) Community calcification rate (G_{net}) plotted against the daily average temperature for all of the NRR studies. Data points with contemporaneous open sea NO_3^{-1} higher or lower than 0.2 μmol l^{-1} are indicated by open and filled circles, respectively. Grey circles indicate values measured during March 2000 and January 2002 during which extreme weather conditions occurred. (**b**) G_{net} plotted versus the diurnal average temperature in NRR for the period October 2000 to March 2002 (not including the study conducted in Jan. 2002). For each monthly period diurnal average pH and average P_g:R values are indicated. The open sea NO_3^{-1} concentration in each study is also indicated by empty and filled circles for NO_3^{-1} > 0.2 μmol l^{-1} and NO_3^{-1} < 0.2 μmol l^{-1}, respectively. (**c**) Community calcification rate (G_{net}) plotted against diurnal average degree of aragonite saturation (Ω_{arag}) calculated as a function of the daily average AT, pH, T and S using the apparent thermodynamic carbonate system dissociation constants according to Mehrbach et al. (1973) and the $CaCO_3$ solubility product according to Mucci (1983). Data points are indicated also by their contemporaneous open sea NO_3^{-1} concentrations >0.2 μmol l^{-1} (empty circles) and <0.2 μmol l^{-1} (filled circles). Calculated linear trend lines are indicated by the black lines passing through the data points. (**d**) Community calcification rate (G_{net}) plotted versus diurnal average global radiation (GR) measured at IUI pier above the sea surface for each study (Table 1) not including 3/2000 and 1/2002

November–December, pH and P_g:R start to rise but G_{net} still decreases with temperature. In the period January–February, NO_3^{-1} values in the open sea are highest, P_g:R and pH are higher than summer and early winter values, and G_{net} appears to rise even though the temperature is falling. During March the pH is still high but slightly lower than the preceding period, NO_3^{-1} levels are very low and G_{net}, even though the temperature is still low, is higher by a factor of ~1.7 than G_{net} during November–December when the temperature was the same and NO_3^{-1} in the open sea was higher than 0.2 μmol l^{-1}. pH should decrease with temperature if seawater is in equilibrium with atmospheric CO_2. However, during November–February pH rises in response to the increase in excess production both of the reef community (P_g:R > 1, Fig. 7a) and open sea phytoplankton community (Fig. 3). The coincidental increase in pH and attenuation of the dependence of G_{net} on temperature suggests that G_{net} is responding directly to changes in the carbonate system, e.g. aragonite degree of saturation (Ω_{arag}) in addition to changes in temperature itself. It should be noted that changes in Ω_{arag} with temperature in a system, which is open to the atmosphere (i.e. constant pCO_2 at 365 μatm), are caused mostly by changes in carbonate ion concentration.

G_{net} is weakly and positively correlated with diurnal average Ω_{arag} (Fig. 8c). However, sorting the data points according to their open sea NO_3^{-1} concentration above and below 0.2 μmol l^{-1}, yields two improved regression lines. G_{net} in the range $\Omega_{arag} = 3.6$–4.4 according to these relations decreases by 30% on average under high relative to low NO_3^{-1} conditions. The two data points appearing at the bottom of Fig. 8a were measured in March 2000 and January 2002, a day after extreme weather conditions, cloudy skies, rough sea, very strong wind and a little rain as well, which occurs very rarely in Eilat. Therefore, these points were considered anomalous and were not included in the rest of Fig. 8 or the correlation statistics calculations for data in Fig. 8c.

Discussion

Chlorophyll *a* and NO_3^{-1} during the winter in the open water of the northern Gulf of Eilat (Fig. 3) fall well above the threshold values indicating eutrophic conditions as defined by Bell (1992) for the GBR lagoon. Nonetheless, the 0.2 μmol l^{-1} threshold for open sea NO_3^{-1} used to separate data points in Figs. 7 and 8 merely indicates the difference between winter eutrophic and summer oligotrophic conditions as reflected by the NRR's P_g:R and open sea productivity measurements (Iluz 1997). All G_{net} values measured between 2000 and 2002 at the NRR are lower than those measured on Indo-Pacific reefs as well as other Red Sea reefs by a factor of 2–4 (Kinsey 1985; Pichon 1997; Silverman et al. 2004). Additionally measurements made during the early 1990s on the same reef are higher by a factor of 2–3 relative to the current rates (Barnes and Lazar 1993; Silverman et al. 2004). These exceptionally low rates probably reflect the substantial loss of live coral cover over the past decade (ca. 70% since the beginning of the 1990's) due mostly to anthropogenic eutrophication (Loya 2004; Silverman et al. 2004, 2005). Nevertheless, the seasonality of metabolic performance observed in this study is consistent with that observed in the early 1990's in the NRR (Silverman et al. 2004), i.e. winter values of G_{net} are lower than summer values, and winter values of P_g:R are higher than in the summer. Similar seasonality in G_{net} was reported for other reefs in the Indo-Pacific as well (Table 4, Smith 1981; Kinsey 1985; Barnes 1988; Pichon 1997). Therefore, it seems reasonable to assume that the seasonal variation in metabolic performance of the NRR reflects the seasonal variations in environmental conditions and not the disturbed state of the reef.

The seasonality in G_{net} values presented in Table 4 was attributed to changes in solar irradiance and temperature (Smith 1981; Kinsey 1985; Pichon 1997). P_g:R did not vary much on these reefs and remained within a relatively narrow range of variance (ΔP_g:R = 0.1–0.4) between summer and winter. Furthermore, variations in

Table 4 Seasonal variation (S-Summer, W-Winter) of metabolic performance values measured on different reefs in the Indo-Pacific since the 1970's reproduced from Smith (1981)[a], Kinsey (1985)[b], Barnes (1988)[c] and Pichon (1997)[d]

Site	Latitude	Season	P_g*	R*	P_n*	P_g:R	G_{net}*
Lizard Is.[b]	15 °S	S	810	980	–180	0.8	90
		W	340	320	30	1.1	70
Tiahura[d]	17 °S	S	640	640	0	1.0	240
		W	830	750	80	1.1	190
Davies Reef[c]	19 °S	S	700	580	120	1.2	160
		W	530	630	–100	0.8	120
Kaneohe Bay[b]	21 °N	S	920	1260	–340	0.7	280
		W	460	530	–80	0.9	220
One Tree Is.[b]	23 °S	S	750	660	180	1.1	130
		W	300	440	–140	0.7	110
French Frigate Shoals[b]	25 °S	S	710	410	300	1.7	280
		W	360	220	140	1.6	80
Abrolhos Atoll[a]	29 °S	S	1750	1630	120	1.1	500
		W	1010	1200	–190	0.8	130

*Metabolic rates are in mmol C m^{-2} day^{-1}

G_{net} values appear to be unrelated to P_g:R values unlike the NRR, which generally exhibited high G_{net} at low P_g:R and low G_{net} at high P_g:R (Figs. 6, 7c). It is likely that the seasonal variations in G_{net} in the Indo-Pacific reefs occurred as a result of seasonal variations in temperature and Ω_{arag} as in the NRR. P_g:R in these studies may be changing in response to the seasonality in the nutrient supply, which may be different in each of the other reefs.

In the NRR G_{net} appears to increase with temperature except in the range 20–23°C (Fig. 7a, b) where it has an inverse trend. This can be explained by the observed increase in average pH associated with the nutrient enrichment and higher open water productivity during the winter mixing, and the associated increase of P_g:R within the reef (Fig. 7b). Ferrier-Pages et al. (2000) showed that single corals that were exposed to high nutrient levels (ammonium and phosphate) decreased their calcification. However, this decrease became smaller as P_g:R of the coral increased with exposure time. This increase in P_g:R may have caused an increase in Ω_{arag}, which countered the effect of nutrients on calcification, perhaps similar to the ecosystem level observations in the NRR. The decrease in G_{net} during the winter, which was associated with high nutrient levels (Figs. 7d, 8a–c) is also in agreement with the findings of Marubini and Davies (1996), who measured the effect of nitrate enrichment (1–20 μmol l^{-1}) on coral growth (*Porites porites* and *Montastrea annularis*) in laboratory experiments. In their study, enrichment of 1, 5 and 20 μmol l^{-1} caused a decrease of 25% and 50% in calcification respectively. As a control, they used corals, which were kept at low NO_3^{-1} (0.05 μmol l^{-1}). In addition, there was a 30–90% increase in net photosynthesis as well as a decrease in dark respiration as NO_3^{-1} increased from 0.05 to 20 μmol l^{-1}, for both species tested. We observed similar changes in response to nutrient enrichment at community level, suggesting that hermatypic corals may be an important component in the measured response of the ecosystem. Finally, recent laboratory studies on individual corals and mesocosms, which tested the combined effect of nitrate enrichment and changes in Ω_{arag} (Marubini and Atkinson 1999; Langdon and Atkinson 2005) indicated that this enrichment suppressed the dependence of calcification on Ω_{arag}. These findings are also in agreement with our in situ observations of a natural coral reef community.

The suppression of G_{net} as a function of Ω_{arag} under high NO_3^{-1} conditions (Fig. 8c) may be attributed to decrease in coral calcification. Alternatively, or in parallel, it may be caused by increase in $CaCO_3$ dissolution under increased nutrient load. Indeed, high nutrients and increased open sea productivity were associated with increased activities of boring organisms within the reef framework (Hallock 1988; Glynn 1997; Zubia and Peyrot-Clausade 2001; Tribollet and Langdon 2004), which could contribute to $CaCO_3$ dissolution (e.g. Lazar and Loya 1991). Finally, G_{net} appears to be unrelated to the daily average global radiation measured in Eilat (Fig. 8d). This is surprising in view of the well documented light enhanced calcification in corals as well as in community metabolism (e.g. Barnes and Chalker 1990 and our own diurnal cycle in G_{net}, Fig. 4c, d). This lack of correlation may be explained by the overriding influence of other environmental parameters on calcification (mainly temperature, carbonate chemistry and nutrients), which are not in phase with the annual radiation cycle. For example, maximum temperature lags behind radiation by roughly 3 months.

In conclusion community metabolism in the NRR reflects the annual eutrophication cycle in the Gulf of Eilat. The seasonal variations in metabolic rates of G_{net} and P_g:R correspond to variations in open sea NO_3^{-1}, diurnal average temperature and Ω_{arag}. P_g:R is positively correlated with NO_3^{-1} and G_{net} is correlated with Ω_{arag} and temperature. The dependence of G_{net} on temperature appears to be caused mainly by its effect on Ω_{arag}. Nutrient enrichment above a threshold of $NO_3^{-1} = 0.2$ μmol l^{-1}, suppressed G_{net} on average by 30% within the range of measured Ω_{arag}. Clearly, the reduction in net deposition of $CaCO_3$ as a result of nutrient enrichment will compromise the integrity of the coral reef framework. Together with increasing P_g:R, which indicates the growing dominion of benthic autotrophs, both processes contribute to the deterioration of such ecosystems. The decrease in calcification under high nutrient load may be due to increased bioerosion (Glynn 1997) and inorganic dissolution of the reef framework or because of competition with photosynthesis of coral algal symbionts for the limited supply of dissolved inorganic carbon as suggested by Dubinsky et al. (1990). Many coral reefs around the globe are situated near inhabited coastal areas, which suffer from nutrient pollution due to changes in land use (agriculture), mariculture, sewage and urbanization. This may cause an additional burden to the survival of coral reefs in view of bleaching and increased atmospheric CO_2 (Buddemeier et al. 2004).

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