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Abundance and trophodynamics of surface microbial loop populations in the northern Red Sea

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The population densities of filter feeding ciliates in the water of the three marine protectorates of Ras Mohammed, Nabq and Abu Galoum in the northern Red Sea, were calculated during the period from November 2006 to November 2007. Also, autotrophic nanoflagellates, heterotrophic nanoflagellates and heterotrophic bacteria were enumerated to gain some indication of the food resources available for ciliates. The abundance of ciliates in the three protectorates were found to follow an annual cycle with the highest ciliate numbers of 25.3 cells ml^{-1} observed in the spring, and the lowest numbers of 2.1 cells ml^{-1} in the summer. Abundances were at times 8-fold higher than those found in comparable studies on nutrient-poor pelagic systems and, astonishingly, approached those observed in coastal waters and in more productive open ocean systems. Nanoflagellates that could provide a food supply for the filter feeding ciliates were especially numerous in the spring, while the production of bacteria was presumably a more important component at the base of this food chain in the three protectorates' water. The filtration activities of heterotrophic flagellates and filter feeding ciliates were compared with the population densities of bacteria, nanoflagellates and ciliates in spring and summer. Moreover, filtration rates from the literature were used to calculate the potential rate of capture of prey of different categories, as well as to calculate the time required for the whole water body to be filtered by heterotrophic nanoflagellates and filter feeding ciliates.

Keywords: nanoflagellates, ciliates, bacteria, natural protectorates and marine parks, Gulf of Aqaba

Introduction

Between 1983 and 1992, the Egyptian Government declared three protected areas in the Gulf of Aqaba at the northern end of the Red Sea, namely, Ras Mohammed, Nabq and Abu Galoum (Law 102 of the year 1983 issued by the Ministry of State for Environmental Affairs-Egyptian Environmental Affairs Agency, MSEA-EEAA). The establishment of these marine protectorates has been viewed as an important opportunity to investigate the contribution of coral reef ecosystems to the productivity of the coastal waters of the Gulf of Aqaba.

There is now a particularly urgent need to acquire a full knowledge of the function of coral reefs and the stability of pelagic ecosystems in the Red Sea before they are disturbed by human activity. The offshore exploitation of oil and gas fields is increasing in this region, and rapid urbanization and industrialization in the coastal zones has already produced localised effects on the susceptible reef ecosystem. To protect the Red Sea biota, an evaluation of the

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intact ecosystem has to be made before the onset of any further disturbance. The investigation reported in this article of the structure and diversity of the microbial populations in the northern Red Sea's marine protectorates is, therefore, part of a wider project aimed at studying the abundance and diversity of different biota in these reserves.

An important issue in the aquatic microbial ecology is the dynamics of the bacterial trophic level in relation to natural predators. These bacteria live floating in seawater and utilize dissolved organic matter, absorbing it directly from their surroundings. In their turn, they are eaten by flagellates and ciliates which themselves are then eaten by small zooplankton (Fenchel, 1988; Sanders et al., 1992; Simon et al., 1992; Hwang and Heath, 1997, 1999). Within the food chain of bacteria-flagellates-ciliates, about 60–70 % of primary production in the open oceans may be ingested by heterotrophic flagellates and ciliates, constituting the so-called "microbial loop" (Pomeroy, 1974). This "loop" may really be an almost closed circuit, with little energy passing to the larger copepods, and may thus represent a parallel food chain to the conventional "grazing" chain of phytoplankton-zooplankton-fish. The details of these linkages and the rates of the processes involved in the microbial loop are still being studied. Indeed, its existence was not known to biological oceanographers until very recently (Pace et al., 2004; Joaquim-Justo et al., 2006; Munawar et al., 2009; First and Hollibaugh, 2010; Munawar et al., 2010).

For this study we chose three convenient sampling sites in the Gulf of Aqaba: the first in Ras Mohammed protectorate, the second in Nabq protectorate and the third in Abu Galoum protectorate. For each of the three sites we followed the changes in abundance of ciliates in near-surface waters during the high water tides throughout one year of sampling. We also estimated the abundance of flagellates and bacteria and followed changes in chlorophyll *a* to gain some understanding of the trophic relationships of ciliate communities in the Gulf. Moreover, filtration rates were used to calculate the potential rate of capture of prey of different categories, as well as to calculate the time required for the whole water body at each protectorate to be filtered by flagellates and ciliates as a means of estimating the efficiency of the ecosystem in each protectorate. The strong correlation between ciliates and chlorophyll *a* predicted that low phytoplankton biomass in nutrient-poor waters should be accompanied by low ciliate abundance (Pitta et al., 2001). Therefore, we expected ciliate abundance in the Gulf of Aqaba to be rather low.

Materials and Methods

Area of study

The Red Sea is a long narrow sea between northeast Africa and the Arabian Peninsula. It has a maximum length of 2250 km, maximum width of 355 km and average depth of 490 m. At the northern end of the Red Sea, lies the Sinai Peninsula bounded on either side by the Gulf of Suez and the Gulf of Aqaba (Morcos, 1970).

The Gulf of Aqaba is an arm of the Red Sea between the Sinai Peninsula and northwest Saudi Arabia. It extends for 180 km from the straits of Tiran to Taba. At its northern limit, it is 5 km wide and reaches a maximum width of 28 km opposite Dahab. There are two major marine basins: the northern one extending south to Nuweiba with a maximum depth of 1000 m, and the southern one which extends to the Strait of Tiran and sounds 1800 m. Within a short distance from the coast, the Gulf has hydrographic conditions resembling those of the open ocean, with no discernible coastal effects on the nutrient regimes and plankton biology. The climate in this area is hot and dry. Rainfall is scarce (averaging 22 mm $year^{-1}$). Evaporation is exceptionally intense (average 200 cm $year^{-1}$) (Godeaux, 1986), and thus the water is hypersaline. The Gulf has been described as highly oligotrophic on the basis of the chlorophyll *a* values and primary productivity measurements carried out by several investigators (Kimor, 1990; Claessens et al., 2008, 2010).

Three nearshore sites were chosen for this study (Figure 1). Site one (1) was chosen in the immediate neighbourhood of the Ras Mohammed area which is known to have more nutrients and detritus from mangrove trees and coral reefs and whose waters are -affected by diving boats and crowded by snorkelers and divers all year-round. The depth of water at this site was 430 m. Site two (2) was chosen within the Nabq protectorate which is bordered by mangroves (*Avicennia marina*) and is affected by the discharge of drainage water from a local shrimp fish farm. The depth of the water at this site was 280 m. Finally, site three (3) was chosen in the vicinity of the Abu Galoum protectorate. The depth of the water at this site was 315 m.

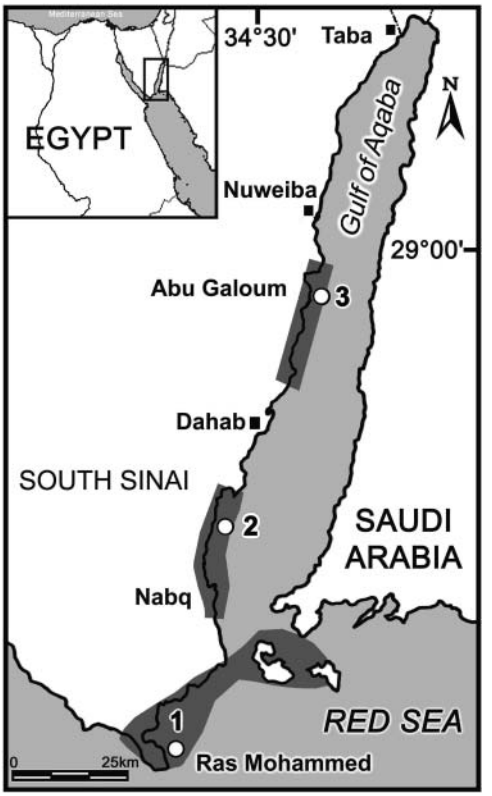

Figure 1. A map of the Gulf of Aqaba showing the location of the three sampling stations (circles) at the marine natural protectorates of Ras Mohammed, Nabq and Abu Galoum (shaded areas). The inset shows the position of the Gulf of Aqaba on the Red Sea.

Sampling and laboratory techniques

Each site was visited twice a month during the stand of high water during high tide, for 13 months extending from November 2006 to November 2007. Sampling was carried out in the vicinity of the coral reef area during the stand of high tide. On each sampling visit three separate samples of 800 ml each were collected from a depth of about 25 cm in glass jars which were then closed with plastic tops. A volume of 180 ml was taken from each bottle, after gentle but thorough mixing and fixed with Lugol's iodine solution (Throndsen, 1978) to a final concentration of 1 %. A further 100 ml was taken from each bottle of the well-mixed sample and fixed with 10 ml of 25 % glutaraldehyde (filtered through a 0.22 μm filter). Fixed subsamples of both types were stored in the dark at 4ºC.

Ciliates in the Lugol's-fixed samples were counted after settlement using the Utermöhl method (Utermöhl, 1958). The preserved samples were gently stirred and poured into three 65 ml settling cylinders, each mounted on a shallow circular trough whose base was formed from a cover glass 25 mm in diameter. The samples were left to stand for at least 12 h before the supernatant was carefully removed and the base was transferred to enable the examination of the settled plankton using a Wild M40 inverted microscope (with phase contrast) at a magnification of x 400. Three subsamples were examined per bottle and three bottles per collection. There were nine replicate counts per site sampled; the counts were expressed as numbers per litre of water.

In order to estimate the numbers of bacteria and nanoflagellates in the samples two 2 ml subsamples of each thoroughly mixed glutaraldehyde fixed water sample were taken. Each subsample was then separately mixed with 0.6 ml of 0.3% DAPI (4′6-diamidino-2-phenylindole (Sigma)) stain (Porter and Feig, 1980) which had been filtered through a 0.22 μm filter in order to remove particles. The mixture was kept in the dark for 7 min before being filtered onto a 0.2 μm pore diameter black polycarbonate filter, using a filter pressure of no more than 10 mm Hg. The filter was mounted on a slide with Gurr's Univert immersion oil (BDH, Poole, England) and examined at x1000 with an Olympus BH-2 microscope fitted with a reflection fluorescence attachment. Bacteria and the nuclei of nanoplanktonic flagellates emitted a blue fluorescence with DAPI, and could be distinguished easily from one another, while autotrophic flagellates showed a red fluorescence from chloroplasts. These three categories of organisms were counted in 20 microscope fields on each filter in order to estimate the number of each type per ml of original sample. There were 6 replicate counts per site on each sampling visit.

These smaller microorganisms were enumerated in order to gain some indication of the food resources available for ciliates. In this respect the filtration activities of the heterotrophic flagellates and ciliates were compared with the population densities of bacteria, flagellates and filter feeding ciliates in a simple table, drawing data from collections at the three protectorates in spring and summer. Filtration rates from the literature (Heinbokel, 1978; Fenchel, 1982; Jonsson, 1986) were used to calculate the potential rate of capture of prey of the different categories, and the time required for the whole water body to be filtered by flagellates and ciliates.

On each sampling visit the temperature of the water was measured at the point of sampling with a thermometer calibrated to 0.1°C.

The salinity of samples was routinely measured by titration against standard silver nitrate and periodically cross-checked with a salinometer bridge (MCS, Electronic Switchgear, London).

The chlorophyll *a* content of the water was also measured. Three 250 ml water samples from each site were filtered separately through 25 mm diameter Whatman glass fibre filters (GF/F). Chlorophyll pigments were extracted from the homogenized filters with 90% acetone. The extract was centrifuged at 2000 rpm for 5 min and the supernatant was made up to 25 ml with 90% acetone. The fluorescence of the extract was measured with an Amincofluorometer that had been calibrated against standard concentrations of chlorophyll *a* (Parsons et al., 1984) and the chlorophyll concentration in the water samples was calculated.

The statistical test, analysis of variance, one factor AVOVA (Underwood, 1981) was followed. The least significant difference test (Steel and Torrie, 1986) was applied to test whether the density of the different microbial groups varied significantly between sites and seasons.

Results

Temperature, salinity and chlorophyll *a* in surface water

Surface water temperature dropped to 13.8°C at site (1) during winter, and rose to 32°C at site (3) during late summer (Figure 2a). The salinity at each site varied with the seasons in the same general manner as the temperature. The range of salinity in high-tide samples at site (1) ranged between 38.8 and 42.5‰; at site (2) between 40 and 42.9 ‰ and at site (3) between 40 and 43‰ (Figure 2b).

Chlorophyll *a* concentrations in water samples from the three sites varied seasonally as shown in Figure 2c. The levels of chlorophyll *a* were consistently higher at Ras Mohammed and Nabq than at Abu Galoum. The highest levels at each of the three sites were recorded during the spring season when chlorophyll *a* concentrations at site one (0.8 μg l^{-1}) were two and four times higher than at sites two and three, respectively.

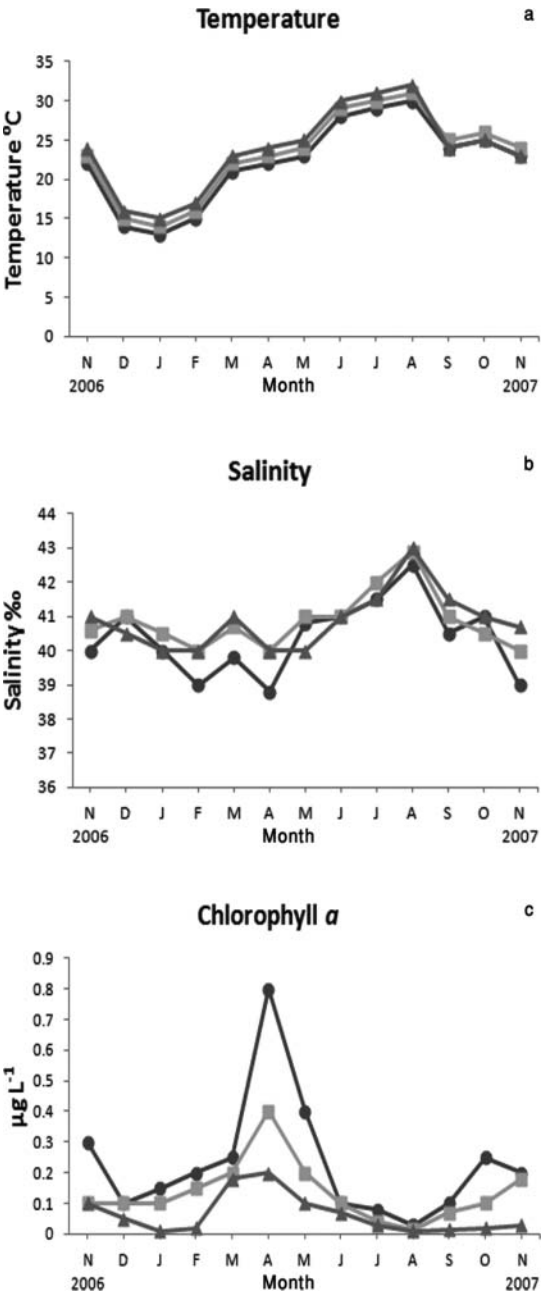

Figure 2. Measurements made on samples collected at Ras Mohammed (circular symbols), Nabq (square symbols) and Abu Galoum (triangular symbols) in the period from November 2006 to November 2007. (a) The mean temperature (°C) recorded from water samples collected from the three sites in each month. (b) The mean salinity values (‰) measured in samples from the three sites in each month. (c) The mean concentrations of chlorophyll *a* (μg l^{-1}) measured in samples from the three sites in each month.

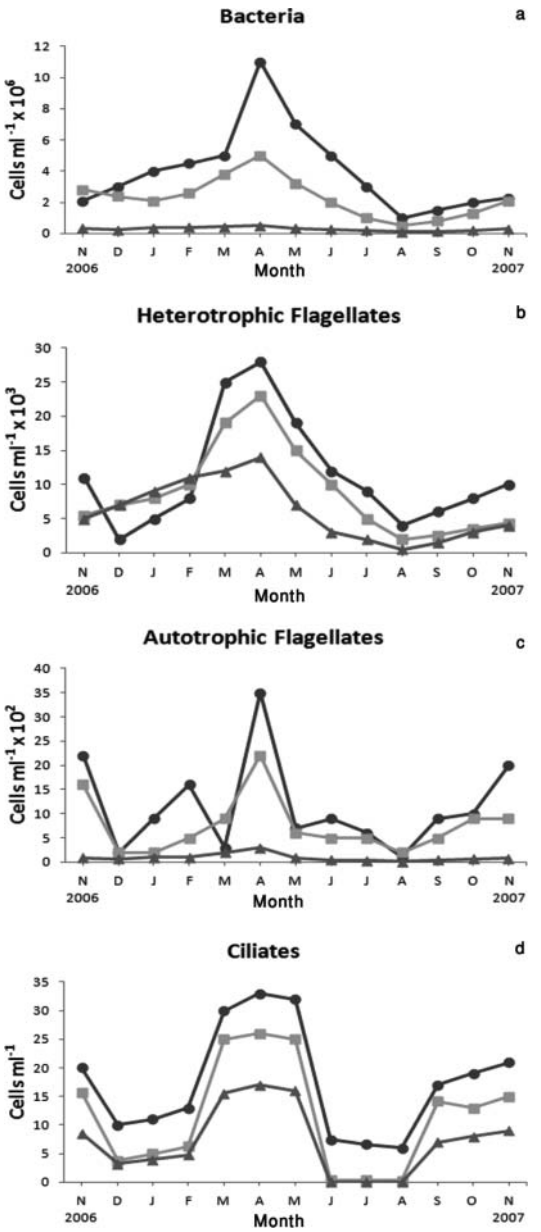

Figure 3. The mean population density of ciliates and non-ciliate microorganisms in samples from the surface waters of Ras Mohammed (circular symbols), Nabq (square symbols) and Abu Galoum (triangular symbols), for each month of the study. (a) Bacteria; (b) heterotrophic flagellates; (c) autotrophic flagellates; (d) ciliates.

Ciliates, flagellates and bacteria

The annual cycle of variation in the abundance of ciliates and non-ciliate microorganisms in the surface waters at the three sites is shown in Figure 3. The population densities of ciliates at Ras Mohammed were consistently higher than those of Nabq and Abu Galoum, with the highest values of 33 ind. ml^{-1} at site one (i.e. Ras Mohammed) during spring, and the lowest values of 0.02 ind. ml^{-1} at site 3 (i.e. Abu Galoum) during summer.

Fluctuations in the abundance of bacteria (Figure 3a) followed the same general trends as those of ciliate numbers. The waters in the Abu Galoum protectorate contained the lowest bacterial population density (0.1 bacteria $\times$ 10^6 ml^{-1}), while the water samples of Ras Mohammed (site 1) contained the highest values (11 bacteria $\times$ 10^6 ml^{-1}).

The abundance of heterotrophic nanoflagellates was very similar across the three sites in spring (Figure 3b), but their numbers were generally lower at sites two (23 ind. $\times$ 10^3 ml^{-1}), and three (14 ind. $\times$ 10^3 ml^{-1}) than at site one (28 ind. $\times$ 10^3 ml^{-1}). The numbers of autotrophic flagellates at the three sites were at least an order of magnitude lower than the numbers of heterotrophic forms at the same site (Figure 3c) and very low numbers of autotrophic flagellates were found in samples from Abu Galoum, i.e. site (3) (0.1 cells $\times$ 10^2 ml^{-1}).

A marked decline in the microbial loop population densities from southern sites towards northern ones was noticed (Figure 4). The average annual number of ciliate individuals at site (2) decreased to 11.5 ind. ml^{-1}, then to 7.2 ind. ml^{-1} at site (3); bacterial population densities decreased to 2.276 cells $\times$ 10^5 ml^{-1} at site (2), then decreased to a lowest density of 0.292 cells $\times$ 10^5 ml^{-1}at site (3); while the density of the population of heterotrophic nanoflagellates decreased from 8.83 ind. $\times$ 10^3 ml^{-1} at site 2 to 6.076 ind. $\times$ 10^3 ml^{-1} at site 3 and, finally, autotrophic nanoflagellates decreased from 7.46 ind. $\times$ 10^2 ml^{-1} at site (2) to 0.95 ind. $\times$ 10^2 ml^{-1} at site (3).

The main annual peak of the microbial population abundances was recorded in April (38.5 bacteria $\times$ 10^5 ml^{-1}; 21.66 ind. $\times$ 10^3 ml^{-1} and 20 ind. $\times$ 10^2 ml^{-1} for heterotrophic and autotrophic nanoflagellates, respectively, and 25.3 ciliates ml^{-1}),; whereas August harboured the lowest densities (3.53 bacteria $\times$ 10^5 ml^{-1}; 2.16 ind. $\times$ 10^3 and 1.03 ind. $\times$ 10^2 ml^{-1} for heterotrophic and autotrophic nanoflagellates, respectively and 2.1 ciliates ml^{-1}) (Figure 5).

These smaller micro-organisms were enumerated in order to gain some indication of the food resources available for ciliates in the water of the

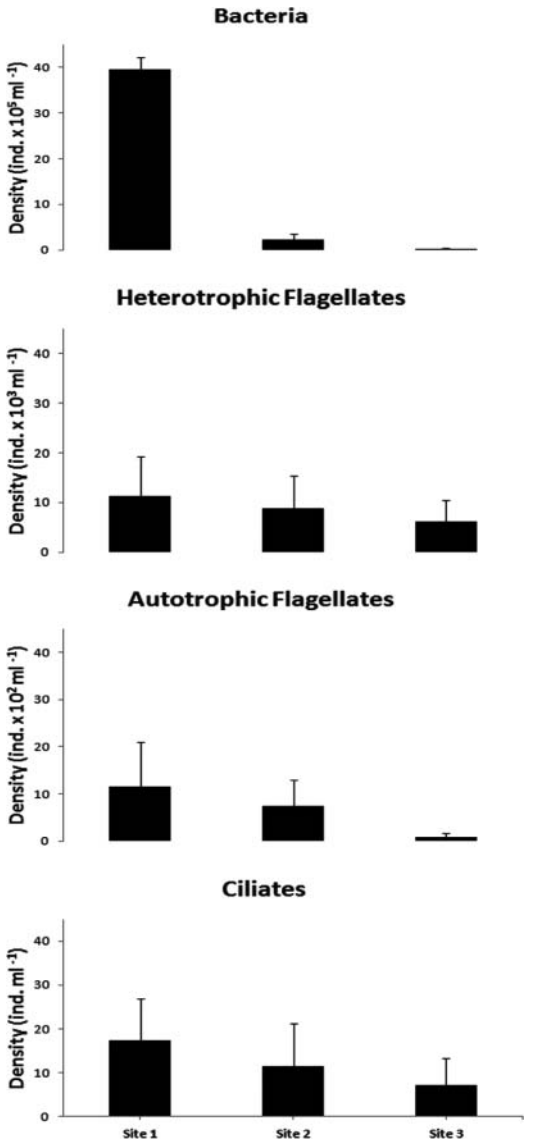

Figure 4. Site variations of the microbial population densities (ciliates, autotrophic nanoflagellates, heterotrophic nanoflagellates and bacteria) at the Gulf of Aqaba (November 2006–November 2007).

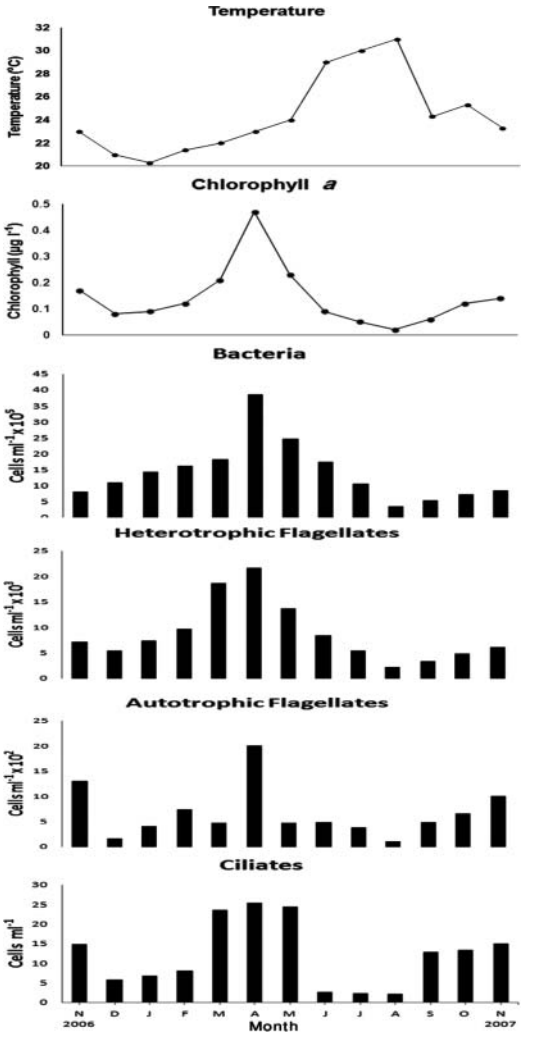

Figure 5. Annual variation of microorganisms (ciliates, autotrophic nanoflagellates, heterotrophic nanoflagellates and bacteria) at the Gulf of Aqaba (November 2006–November 2007).

three protectorates. In this connection, the filtration activities of the heterotrophic flagellates and ciliates, together with the population densities of bacteria, flagellates and filter feeding ciliates were compared, as described in Table 1, drawing data from collections at the three protectorates in spring and summer. Filtration rates from the literature were used to calculate the potential rate of capture of prey of the different categories, and the time required for the whole water body of each protectorate to be filtered by flagellates and ciliates. The importance of the heterotrophic nanoflagellates as consumers of bacteria was assessed by multiplying their numbers in nature with the determined values of clearance derived from the literature. The potential rate of food capture by flagellates decreased from 110 bacteria h^{-1} at site (1) to just one bacterium h^{-1} at site (3). During spring, the high population of nanoflagellates filters the whole water body of Ras Mohammed (site 1) 6 times a day. This filtration activity, however, decreased by half at Abu Galoum (site 3).

It is clear that there is a highly significant difference in the microbial density between the three

Table 1. A comparison of the bacterial, total nanoflagellates (TNAN), heterotrophic nanoflagellates (HNAN) and filter-feeding ciliate populations with estimates of the clearance rates and potential rates of food capture by these flagellates and ciliates during spring and summer 2007 at Ras Mohammed (R.M.), Nabq (N.) and Abu Galoum (A.G.) protectorates.

	Spring 2007			Summer 2007		
	R.M.	N.	A.G.	R.M.	N.	A.G.
Bacteria						
Bacteria numbers (cells 1^{-1})	11×10^9	5×10^9	5×10^9	1.0×10^9	0.5×10^9	1.0×10^9
Flagellates						
TNAN numbers (cells 1^{-1})	3.15×10^7	2.52×10^7	1.43×10^7	0.41×10^7	0.22×10^7	0.051×10^7
HNAN numbers (cells 1^{-1})	2.8×10^7	2.3×10^7	1.4×10^7	0.4×10^7	0.2×10^7	0.05×10^7
Volume cleared/ HNAN/hour* (1 h^{-1})	10^{-8}	10^{-8}	10^{-8}	10^{-8}	10^{-8}	10^{-8}
Bacteria encountered/ HNAN (cells h^{-1})	110	50	5	10	5	1
Volume cleared by HNANs in each litre in an hour (1)	0.28	0.23	0.14	0.04	0.02	0.005
Time for HNANs to filter whole Water body (h)	3.57	4.3	7.14	25	50	200
Ciliates						
Filter feeding ciliate numbers (cells 1^{-1})	33,000	26,000	17,000	6000	300	20
Volume filtered/ciliate/ hour** (1 h^{-1})	5×10^{-6}	5×10^{-6}	5×10^{-6}	5×10^{-6}	5×10^{-6}	5×10^{-6}
Bacteria filtered/ciliate/ hour (cells h^{-1})	55,000	25,000	2500	5000	2500	500
TNAN filtered/ciliate/ hour (cells h^{-1})	157.5	126	71.5	20.5	11	2.55
Volume filtered by ciliates in each litre in one hour (1)	0.165	0.13	0.085	0.03	0.0015	0.0001
Time for ciliates to filter whole Water body (h)	6.06	7.69	11.76	33.33	666.66	10,000

*Mean value from Fenchel (1982). **Mean value for a range of tintinnids and non-loricate oligotrichs in data by Heinbokel (1978) and Jonsson (1986).

sites ($p < 0.05$). The ANOVA test also showed that season had no significant effect on the density of microbial communities in the three sites. The value of p was >0.05 for all groups.

Discussion

The abundance of ciliates at the three sites with values of 17.4 cells ml^{-1} (site 1); 11.5 cells ml^{-1}

(site 2) and 7.2 cells ml^{-1} (site 3), showed a progressive decline in population densities moving northward along the Gulf. This indicated that the surface waters of the northern protectorate of Abu Galoum (site 3) were less productive, when compared with the southern protectorates of Ras Mohammed (site 1) and Nabq (site 2). It is suggested that this was due to the lower level of nutrient and detritus substances at Abu Galoum. The southern protectorates of Ras Mohammed and Nabq were characterized by the presence of mangrove trees and coral reefs which enhanced the abundance of nutrient and detritus substances. Mangroves provide a unique ecological niche for a range of microorganisms which play various roles in nutrient recycling, as well as various other environmental activities (Sahoo and Dhal, 2009).

While the observations in this study, therefore, broadly agree with the traditional concept of the increasing oligotrophy of the Red Sea water to the north (Kimor, 1990; Claessens et al., 2010), the overall ciliate densities observed were nonetheless significantly higher than previous studies have indicated. The lower ciliate population density at Abu Galoum (site 3), for example, was still two times higher than that found at the northern part of the Gulf of Aqaba (3.5 cells ml^{-1}) in the earlier study by Claessens et al. (2008). Moreover, the densities of ciliate populations in the Gulf of Aqaba were up to eight-fold higher than abundances in other comparable studies in nutrient poor systems (Revelante and Gilmartin, 1990; James and Hall, 1995; Pitta et al., 2001) and were comparable with maximum values found in coastal waters or in more productive open ocean systems (Stoecker et al., 1989; Leakey et al., 1996).

The strong correlation between ciliates and chlorophyll *a* generally predicts that low phytoplankton biomass in nutrient-poor waters should be accompanied by low ciliate biomass (Pitta et al., 2001). However, despite the oligotrophic status of the Gulf of Aqaba, which was accompanied by a very low density of autotrophic nanoflagellates, the ciliate density revealed in this study was unexpectedly high. Moreover, the ciliate abundance was astonishingly high not only during nutrient-replete conditions in spring, but also in summer, when nutrients were strongly depleted (Claessens et al., 2008). These findings suggest both that the ciliate community in the Gulf of Aqaba was much more efficient in utilizing nanophytoplankton as its preferable food sources in all seasons, and that the degree of top-down control (predation) of the ciliate community was relatively low. This hypothesis might explain the unexpectedly high ciliate abundance in this oligotrophic marine habitat.

Turning now to the evidence with respect to the bacterial population, during the present study, bacterial population densities at site (1) were recorded as ranging between 1×10^6 ml^{-1} and 11×10^6 ml^{-1}. This represented a much higher density than that recorded at site (3), which returned values between 0.1 and 0.5×10^5 ml^{-1}. Moreover, site (3) contained the lowest chlorophyll *a* values, especially when compared with those of site (1). These findings, therefore, suggest a correlation between bacterial abundance and chlorophyll *a* concentration in this oligotrophic habitat. In this respect, the findings of this study recall those of Sanders et al. (1992), who stated that there is a strong positive correlation between bacterial abundances on the one hand, and chlorophyll *a* and the trophic state of the aquatic habitat on the other hand. Thus, the reduced number of heterotrophic bacteria at the Abu Galoum protectorate, site (3), can partly be related to the decrease in chlorophyll *a* concentration, which in its turn reflects the more pronounced oligotrophy northward along the Gulf.

The dynamics of the bacterial trophic levels in relation to natural predators and/or food supply in different aquatic microbial ecosystems have been discussed by many investigators (Fenchel, 1987; Billen et al., 1990; Sanders et al., 1992; Simon et al., 1992; Brett et al., 2009; Munawar et al., 2010). The correlation between chlorophyll *a* values and bacterial population densities observed in this study, together with the data in Figure 4, support the supposition that bottom-up control (food supply) was a more important factor in regulating bacterial abundance in this highly oligotrophic site than top-down control (predation). The data represented in Figure 4 demonstrates that, despite a reduction in the absolute abundances of heterotrophic flagellates at site (3) compared to site (1), and therefore a reduction in grazing pressure on bacteria at this site, the bacterial population at site (3) was nonetheless consistently extremely low. In other words, even in a situation where grazing pressure on bacteria at this protectorate (site 3) was reduced due to lower absolute abundances of heterotrophic flagellates, the bacteria were still not capable of rapid increases in abundance. This suggests that bottom-up control, due to substrate limitations, represented a more significant

mechanism controlling the bacterial population in this aquatic oligotrophic ecosystem than top-down control. This conclusion therefore supports that of Billen et al. (1990) and Sanders et al. (1992) that in oligotrophic ecosystems the bacterial population is more strongly controlled by substrate supply.

The trophic relationship between heterotrophic nanoflagellates and the bacterial populations of these marine protectorates can be further illustrated from the data in Table 1. Here it is shown that the number of bacteria that could be caught per flagellate per hour was high in spring (110, 50 and 5 at sites 1, 2 and 3, respectively) and low in summer (10, 5, and 1 for the three sites, respectively). Fenchel (1982) calculated the maximum ingestion rate of 27–254 bacteria flagellate^{-1} hour^{-1}, while Sherr et al. (1983) found ingestion rates of 10-75 bacteria flagellate^{-1} hour^{-1} and Weisse (1989) recorded ingestion rates of 36–94 bacteria flagellate^{-1} hour^{-1}. Using these figures as a basis, it can be concluded that the flagellate population of Ras Mohammed and Nabq protectorates could be able to maintain themselves with these more or less suitable ingestion rates of 10–110 bacteria flagellate^{-1} hour^{-1} and 5–50 bacteria flagellate^{-1} hour^{-1}, respectively. The flagellate populations of Abu Galoum protectorate, however, would surely not be able to maintain themselves with the very low ingestion rate calculated here of just1–5 bacteria flagellate^{-1} hour^{-1}, unless it might be suggested that the heterotrophic nanoflagellates of this protectorate might utilize nanophytoplankton as a food supply as well as bacteria. Microscopic plants and heterotrophic bacteria provide the food for heterotrophic protists in various aquatic habitats (Sleigh, 1989; Hwang and Heath, 1997, 1999).

These smaller microorganisms were enumerated in order to gain some indication of the food resources for ciliates. In this connection the filtration activities of the heterotrophic flagellates and ciliates were compared with the population densities of bacteria, flagellates and filter feeding ciliates in Table 1, drawing data from collections at Ras Mohammed Protectorate (site 1), Nabq protectorate (site 2) and Abu Galoum protectorate (site 3) in spring and summer. Filtration rates derived from the literature were used to calculate the potential rate of capture of prey of different categories of organisms, as well as, to estimate the time required for the whole water body to be filtered by hetrotrophic flagellates and filter feeding ciliates. If the high populations of nanoflagellates do indeed filter the whole body of water every 3, 4 and 7 h in spring at Ras Mohammed, Nabq and Abu Galoum protectorates, respectively, the bacteria must be reproducing quickly in order to maintain their populations, or there must be continuous very active recruitment of bacteria into suspension from sediments and surfaces.

It is recognised that ciliates could also be consuming bacteria but flagellates are a more likely food source for ciliates, and presumably a more "attractive" one, on account of the much greater nutritive value of each cell and the coarser filter required (Fenchel, 1988; El-Serehy and Sleigh, 1993; First and Hollibaugh, 2010). The filter-feeding ciliates in the waters of the Ras Mohammed protectorate were numerous enough during spring to filter the whole water body four times a day, and the ciliate population was therefore surely able to catch enough flagellates during this time to provide for ordinary growth and maintenance of the population. In summer, however, the possible food capture rate per ciliate provided less opportunity for growth. It is conceivable that the balance must depend on the relative sizes of the organisms involved. Rassoulzadegan et al., 1988 found that the tintinnids consume nanoplankton in the 2–20 μm size range, while the smaller oligotrichs ate more picoplankton in the 0.2–2 μm size range. Moreover, Gaedke and Kamjunke (2006) stated that pelagic foodwebs have a unique size-dependency in feeding modes.

Conclusions

The Gulf of Aqaba is regarded by scholars as being among the most oligotrophic marine habitats, with a well established concept of increasing oligotrophy of the gulf water to the north. Despite the oligotrophic status of the Gulf of Aqaba, this study found that the ciliate density in its waters was astonishingly high. Abundances were at times eightfold higher than those found in comparable studies on nutrient-poor pelagic systems and approached those observed in coastal waters, indicating a high efficiency among the ciliate populations in utilizing the available food, and suggesting that the planktonic foodweb in this oligotrophic habitat is dominated by the microbial loop. Statistical analysis has shown that the site, not the season, is the main factor affecting the density of the microbial groups in the three sites. The relatively higher density of the microbial community recorded in the southern protectorate (Ras Mohammed) reflects the diversity of

the reef environment as a whole, and indicates the importance of marine reserves in the protection of biodiversity and providing naturally balanced areas, free from direct human disturbance, which can act as reference areas for the study of natural processes in the marine environment.

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References

Billen, G., Servais, P., Becquevort, S., 1990. Dynamics of bacterioplankton in oligotrophic and eutrophic aquatic environments: bottom –up or top-down control? Hydrobiologia 207, 37–42.

Brett, M. T., Kainz, M. J., Taipale, S. J., Seshan, H., 2009. Phytoplankton, not allochthonous carbon, sustains herbivorous zooplankton production. PNAS 106(50), 21197–21201

Claessens, M., Wickham, S.A., Post, A.F., Reuter, M., 2008. Ciliate community in the oligotrophic Gulf of Aqaba, Red Sea. Aquat Microbial Ecol. 53, 181–190.

Claessens, M., Wickham, S.A., Post, A.F., Reuter, M., 2010. A paradox of the ciliates? High ciliate diversity in a resource-poor environment. Mar Biol. 157, 483–494.

El-Serehy, H. A., Sleigh, M. A., 1993. Ciliates in the plankton of the River Itchen Estuary, England. Acta Protozool. 32, 183–190.

Fenchel, T., 1982. Ecology of heterotrophic microflagellates. IV. Quantitative occurrence and importance as bacterial consumers. Mar Ecol- Prog Ser. 9, 35–42.

Fenchel, T., 1987. *Ecology of Protozoa*. Science Tech, Madison, Wisconsin.

Fenchel, T., 1988. Marine plankton food chains. Annu Rev Ecol Syst. 19,19–38.

First, M.R., Hollibaugh, J.T., 2010. Environmental factors shaping microbial community structure in salt marsh sediment. Mar Ecol- Prog Ser. 399, 15–26.

Gaedke, U., Kamjunke, N., 2006. Structural and functional properties of low and high diversity planktonic food webs. J. Plankton Res. 28 (7), 707–718.

Godeaux, J., 1986. The Gulf of Aqaba, a zone of great biological interest. UNESCO. Tech Papers Mar Sci. 49, 104–106.

Heinbokel, J.F., 1978. Studies on the functional rate of tintinnids in the southern California Bight. II. Grazing rates of field populations. Mar Biol. 47, 191–197.

Hwang, S-J., Heath, R. T., 1997. Bacterial productivity and protistan bacterivory in coastal and offshore communities of Lake Erie. Can. J. Fish. Aquat. Sci. 54, 788–799.

Hwang, S-J., Heath, R. T., 1999. Zooplankton bacterivory at coastal and offshore sites of Lake Erie. J. Plankton Res. 21 (4), 699–719.

James, M.R., Hall,,J.A., 1995. Planktonic ciliated protozoa: their distribution and relationship to environmental variables in a marine coastal ecosystem. J Plankton Res. 17, 659–683.

Joaquim-Justo, C., Pirlot, S., Viroux, L., Servais, P., Thome, J., Descy, J., 2006. Trophic links in the low land river Meuse (Belgium): assessing the role of bacteria and protozoans in planktonic food webs. J Plankton Res. 28 (9), 857–870.

Jonsson, P.R., 1986. Particle size selection, feeding rates and growth dynamics of marine planktonic oligotrichous ciliates (Ciliophora: Oligotrichida). Mar Ecol - Prog Ser. 33, 265–277.

Kimor, B., 1990. Microplankton of the Red Sea, the Gulf of Suez and the Levantine Basin of the Mediterranean. Bull Institut. Océanogr Monaco. 7, 29–38.

Leakey, R.J.G., Burkill, P.H., Sleigh, M.A., 1996. Planktonic ciliates in the northwestern Indian Ocean: their abundance and biomass in waters of contrasting productivity. J. Plankton Res. 18, 1063–1071.

Morcos, S.A., 1970. Physical and chemical oceanography of the Red Sea. Oceanogr. Mar. Biol. 8, 73–202.

Munawar, M., Munawar, I.F., Fitzpatrick, M., Niblock, H., Lorimer, J., 2009. The base of the food-web at the top of the Great Lakes: structure and function of the microbial foodweb of Lake Superior. In: M. Munawar and I. F. Munawar (Eds.), *State of Lake Superior*, pp. 289–318. Ecovision World Monograph Series, Aquatic Ecosystem Health and Management Society, Burlington, ON.

Munawar, M., Fitzpatrick, M., Munawar, I.F., Niblock, H., 2010 . Checking the pulse of Lake Ontario's microbial-planktonic communities: A trophic transfer hypothesis. Aquat. Ecosyst. Health Mgmt. 13 (4), 395–412.

Pace, M. L., Cole, J. J., Carpenter, S. R., Kitchell, J. F., Hodgson, J. R., Van De Bogert, M., Bade, D. L., Kritzberg, E. S., Bastviken, D., 2004. Whole-lake carbon-13 additions reveal terrestrial support of aquatic food webs. Nature 427, 240–243.

Parsons, T.R., Maita, Y., Lalli, C.M. (Eds), 1984. *A manual of chemical and biological methods for sea water analysis*. Pergamon Press, Oxford.

Pitta, P., Giannakourou, A., Christaki, U., 2001. Planktonic ciliates in the oligotrophic Mediterranean Sea: longitudinal trends of standing stocks, distributions and analysis of food vacuole contents. Aquat Microb Ecol. 24, 297–311.

Pomeroy, L. R., 1974. The ocean's food web a changing paradigm. BioScience 24, 499–504.

Porter, K.G., Feig, Y.S., 1980. The use of DAPI for identifying and counting aquatic micro-flora. Limnol. Oceanogr. 25, 943–948.

Rassoulzadegan, F., Laval-Peuto, M., Sheldon, R.W., 1988. Partitioning of the food ration of marine ciliates between pico- and nanoplankton. Hydrobiol. 159, 75–88.

Revelante, N., Gilmartin, M., 1990. Vertical water column resource partitioning by a ciliate protozoan population under

stratified conditiond in the northern Adriatic. J Plankton Res. 12, 89–107.

Sahoo, K., Dhal, N.K., 2009. Potential microbial diversity in mangrove ecosystems: A review. Indian J Mar. Sci 38 (2), 249–256.

Sanders, R.W., Caron, D.A., Berninger, U.G., 1992. Relationships between bacteria and heterotrophic nanoplankton in marine and fresh waters: an inter-ecosystem comparison. Mar. Ecol-Prog Ser. 86, 1–14.

Sherr, B.F., Sherr, E.B, Berman, T., 1983. Grazing, growth and ammonium excretion rates of a heterotrophic microflagellate fed with four species of bacteria. Appl Environ Microb. 45, 1196–1201.

Simon, M., Cho, B.C., Azam, F., 1992. Significant of bacterial biomass in lakes and the ocean: comparison to phytoplankton biomass and biogeochemical implications. Mar. Ecol-Prog. Ser. 86, 103–110.

Sleigh, M. A. (Eds), 1989. *Protozoa and other protists*. Edward Arnold, London.

Steel, R.G.D., Torrie, J.H., 1986. *Principles and procedures of statistics. A biometric approach. Second Edition*. McGraw Hill, Inc.

Stoecker, D.K., Taniguchi, A., Michaels, A.E., 1989. Abundance of autotrophic, mixotrophic and heterotrophic planktonic ciliates in shelf and slope waters. Mar. Ecol-Prog. Ser. 50, 241–254.

Throndsen, J., 1978. Preservation and storage. In: A. Sournia (Ed.), *Phytoplankton Manual*, pp. 69–74. UNESCO, Paris.

Underwood, A.J., 1981. Techniques of analysis of variance in experimental biology and ecology. Oceanogr. Mar. Biol. Ann. Rev. 19, 513–605.

Utermöhl, H., 1958. Zur vervollkommnung der quantitativen phytoplankton methodik. (The improvement of quantitative phytoplankton methodology. In German). Mitt. Int. Verein. theor. angew. Limnol. 9, 1–38.

Weisse, T., 1989. The microbial loop in the Red Sea: dynamics of pelagic bacteria and heterotrophic nanoflagellates. Mar. Ecol-Prog. Ser. 55, 241–250.