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Microbial Loop Populations: Their Abundances and Trophodynamics in the Gulf of Aqaba, Red Sea

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Abstract

Population densities of filter feeding ciliates in the water of the three marine protectorates of Ras Mohammed, Nabq and Abu Galoum in the Gulf of Aqaba at the northern Red Sea, were estimated during the period from November 2006 to November 2007. Also, autotrophic nanoflagellates, heterotrophic nanoflagellates and heterotrophic bacteria were characterised in order to gain some indication of the food resources for ciliates. The abundance of ciliates in the waters of the three protectorates were found to vary according to an annual cycle, with the highest ciliate numbers of $2.5x10^4$ cells L^{-1} occurring in the spring and the lowest numbers of $0.2x10^4$ cells L^{-1} occurring in the summer. Abundances were at times eight-fold higher than those found in comparable studies of nutrient-poor pelagic systems and 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 during spring, and it is confirmed that the production of bacteria is an important component at the base of this food chain in the waters of the three marine protectorates. The study explored these food chain relationships by calculating the potential rate of capture of prey and the clearance rate of heterotrophic nanoflagellates and filter feeding ciliates. The study also compared the filtration rates of heterotrophic flagellates and of filter feeding ciliates.

Keywords: Nanoflagellates, ciliates, bacteria, natural protectorates and marine parks, Gulf of Aqaba, Red Sea.

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: Ras Mohammed, Nabq and Abu Galoum. 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 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 also increasing in the region, and rapid urbanization and industrialization in the coastal zones has already produced localised effects on the susceptible reef ecosystem. In order to protect the Red Sea biota, an evaluation of the intact ecosystem has to be made prior to the onset of further disturbances. This study of the structure and diversity of the microbial populations in the marine protectorates in the Gulf of Aqaba is part of a wider project to record 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. Planktonic bacteria utilize dissolved organic matter, absorbing it directly from their surroundings. They are in turn eaten by flagellates and ciliates which again are then eaten by small zooplankton (Fenchel, 1988; Sanders *et al*., 1992; Simon *et al*., 1992). The food chain of bacteria-flagellates-ciliates may consume about 60-70 % of primary production in the water column (Pomeroy, 1974 and Azam *et al*. 1983). Although the existence of the microbial loop has been known for some time, the precise nature of the linkages and the rates of the processes involved in the microbial loop are still being studied and are only now close to being fully understood by biological oceanographers (Joaquim-Justo *et al*., 2006; First and Hollibaugh, 2010). This "loop" may really be an almost closed circuit, with little energy passing to the larger zooplankton such as

copepods and indeed, might be seen as a parallel food chain to the conventional "grazing" chain of phytoplankton-zooplankton-fish.

For this study, three convenient sampling sites were selected in the Gulf of Aqaba, the first in Ras Mohammed protectorate, the second in Nabq protectorate and the third in Abu Galoum protectorate. The strong correlation between ciliates and chlorophyll *a* predicts that low phytoplankton biomass in nutrient-poor waters should be accompanied by low ciliate abundance (Pitta *et al*., 2001). Since levels of chlorophyll *a* in the Gulf of Aqaba are low it was expected that ciliate abundance in the Gulf of Aqaba would also to be rather low. This hypothesis was tested in the study by following the changes in the abundance of ciliates in near–surface waters during the high water tides throughout one year of sampling. In addition, the abundance of flagellates and bacteria was estimated and changes in chlorophyll *a* were tracked in order 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 of organism, as well as to estimate the time required for the water column at each site to be filtered by flagellates and ciliates.

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.

The Gulf of Aqaba extends for 180 km from the straits of Tiran to Taba. At its northern limit - it is 5 km wide but 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 extending to the Strait of Tiran and sounding 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). Evaporation is exceptionally intense (average 200 cm / year) (Godeaux, 1986) and thus the water is saline. 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 near shore 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 it is affected by boats with divers and crowded by snorkelers and divers all the 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 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 closed by plastic tops. A volume of 180 ml was taken from each bottle. After gentle, but thorough mixing, it was 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 4°C.

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 fitted with phase contrast at a magnification of 400X. 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.

Two 2 ml subsamples of each thoroughly mixed glutaraldehyde fixed water sample were taken in order to estimate the numbers of bacteria and nanoflagellates. Each subsample was 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 a magnification of 1000X with an Olympus BH-2 microscope fitted with a epifluorescence 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 six 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 water column 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.

Results

Temperature, Salinity and Chlorophyll *a* in Surface Water

Surface water temperature dropped to 19.8°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. 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 concentrations at site (1) were two and four times higher at sites (2) and (3), respectively.

Ciliates, Flagellates and Bacteria

The annual cycle of variation in the abundance of ciliates 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. The highest values at site (1), i.e. Ras Mohammed were recorded during

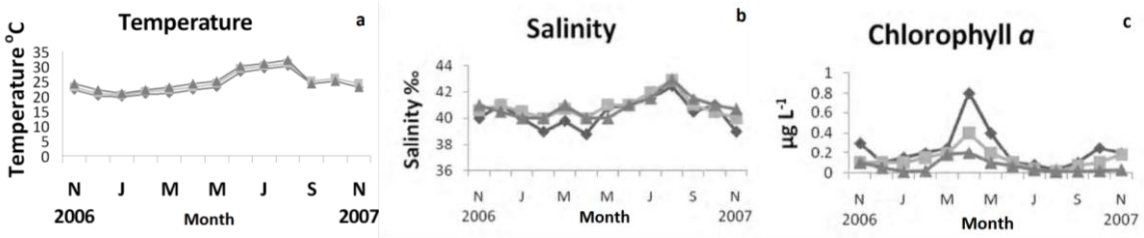

Figure 2. Measurements made on samples collected at Ras Mohammed (diamond symbols), Nabq (square symbols) and Abu Galoum (triangular symbols) in the period from November 2006 to November 2007: a- the mean temperature (°C) recorded from water samples collected from the three sites in each month. b- the 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.

spring and the lowest values at Abu Galoum (Site 3) during summer.

Fluctuations in the abundance of non ciliate micro-organisms (i.e. bacteria, heterotrophic nanoflagellates and autotrophic nanoflagellates) are shown in Figures 4a, 4b and 4c. Fluctuations in the abundance of bacteria (Figure 4a) followed the same general trends as those of ciliate numbers. The waters in the Abu Galoum protectorate contained the lowest bacterial population density, while the water samples of Ras Mohammed (site 1) contained the highest values.

The abundance of heterotrophic nanoflagellates was very similar across the three sites in spring (Figure 4b), but their numbers were generally lower at sites 2 and 3 than at site 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 4c) and very low numbers of autotrophic flagellates were found in samples from Abu Galoum (site 3).

A marked decline in population densities from southern sites towards northern ones was noticed (Figure 5). The average annual number of ciliates at site (2) decreased to $1.15x10^4$ L^{-1}, and to $7.17x10^3$ L^{-1} at site (3); bacterial population densities decreased to $2.28x10^5$ ml^{-1} at site (2), and decreased to a lowest density of $2.92x10^5$ cells ml^{-1} at site (3); while the density of the population of heterotrophic nanoflagellates decreased from $8.83x10^3$ ml^{-1} at site 2 to $6.076x10^3$ ml^{-1} at site 3 and, finally, autotrophic nanoflagellates decreased from $7.46x10^2$ ml^{-1} at site (2) to $0.95x10^2$ ml^{-1} at site (3).

The main annual peak of the microbial population abundances was recorded in April (bacteria: $3.85x10^6$ ml^{-1}; $21.66x10^3$ ml^{-1} and $2x10^3$ ml^{-1} for heterotrophic and autotrophic nanoflagellates, respectively, and $2.53x10^3$ ciliates L^{-1}), whereas August harboured the lowest densities (bacteria: $3.53x10^5$ ml^{-1}; $2.16x10^3$ and $1.03x10^2$ ml^{-1} for heterotrophic and autotrophic nanoflagellates, respectively and 2106 ciliates L^{-1}) (Figure 6).

Microbial densities in oligotrophic pelagic and offshore waters of the Gulf of Aqaba were compared with those of more productive waters around the world (Table 1). The filtration activities of the heterotrophic flagellates and ciliates, together with the population densities of bacteria, flagellates and filter feeding ciliates were compared in spring and summer (Table 2).

Discussion

The abundances of ciliates at the three sites, with values of $1.74x10^4$ cells L^{-1} (site 1), $1.15x10^4$ cells L^{-1} (site 2), and $7.17x10^3$ cells L^{-1} (site 3), showed a progressive decline in population densities northward along the gulf. This indicates that the surface waters of the northern protectorate of Abu Galoum (site 3) are less productive, when compared with the southern protectorates of Ras Mohammed (site 1) and Nabq (site 2). It is suggested that this is due to the decrease of nutrient and detritus substances at Abu Galoum. The southern protectorates of Ras Mohammed and Nabq are characterised by the presence of mangrove trees and coral reefs which seemed to enhance 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 towards north (Kimor, 1990; Claessens *et al*., 2010) the overall ciliate densities observed were 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 (3534 cells L^{-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).

A strong correlation between ciliates and chlorophyll *a* predicts that low phytoplankton biomass in nutrient-poor waters should be

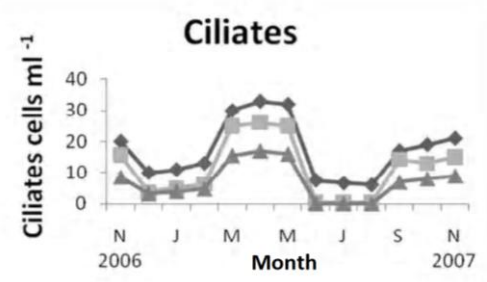

Figure 3. The mean population density of ciliates in samples from the surface waters of Ras Mohammed (diamond symbols), Nabq (square symbols) and Abu Galoum (triangular symbols), for each month of the study.

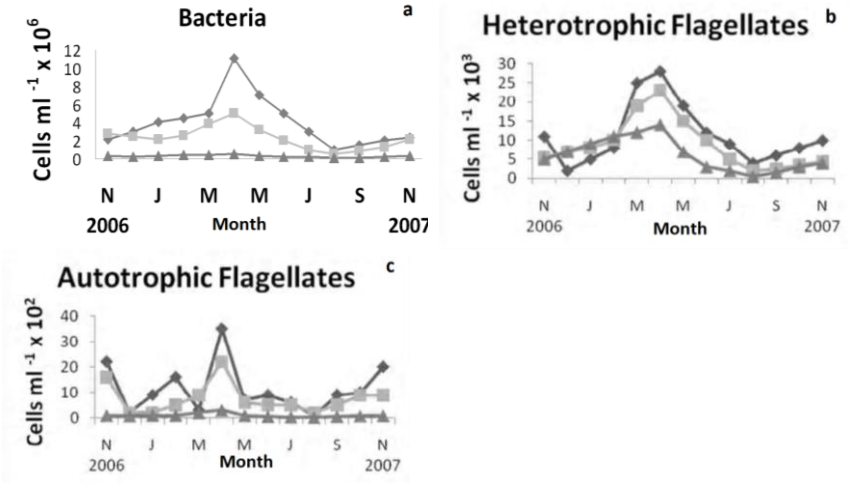

Figure 4. Mean values for the abundance of non-ciliate microorganisms in each month at Ras Mohammed (diamond symbols), Nabq (square symbols) and Abu Galoum (triangular symbols). a- bacteria; b- heterotrophic flagellates; c- autotrophic flagellates.

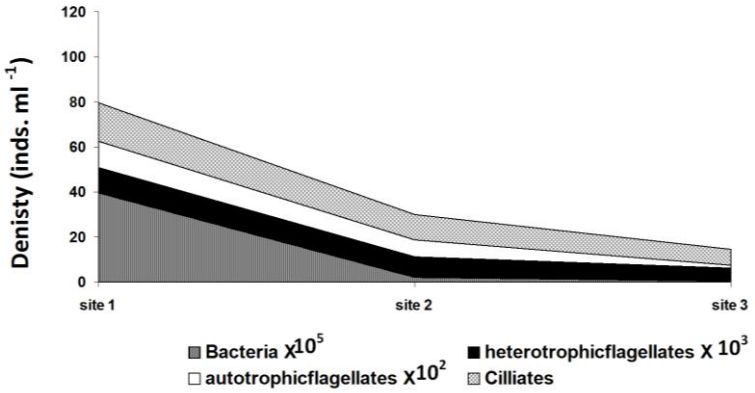

Figure 5. Site variations of the microbial population densities (ciliates, autotrophic nanoflagellates, heterotrophic nanoflagellates and bacteria) in the Gulf of Aqaba (November 2006-November 2007).

accompanied by low ciliate biomass (Pitta *et al*., 2001). However, despite the oligotrophic status of the Gulf of Aqaba, which was supported by very low densities of autotrophic nanoflagellates, ciliate density was unexpectedly high. This was the case not only during nutrient-replete conditions in spring, but also in summer, when nutrients were strongly depleted (Claessens *et al*., 2008). This suggests that the ciliate community in the Gulf of Aqaba is much more efficient in utilizing nanophytoplankton as a food source during all seasons, and that the degree of top-down control (predation) of the ciliate community is relatively low in the gulf (although alternative food sources could be heterotrophic bacteria and heterotrophic nanoflagellates). Although these factors were not evaluated in the present study, this

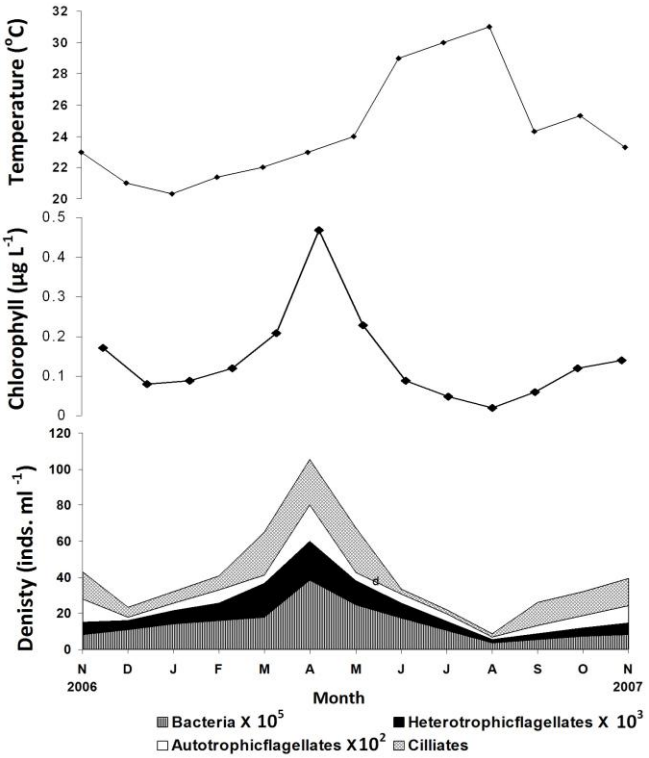

Figure 6. Annual variation of microorganisms (ciliates, autotrophic nanoflagellates, heterotrophic nanoflagellates and bacteria) in the Gulf of Aqaba (November 2006-November 2007).

Table 1. A comparison between the abundance of microbial loop populations in the oligotrophic waters of the Gulf of Aqaba and more productive marine waters around the world

Location	Ciliate abundance ($x10^3$ cells L^{-1})	Flagellate abundance ($x10^3$ cells ml^{-1})	Bacterial abundance ($x10^6$ cells ml^{-1})	Source
Gulf of Aqaba[b]	2.11-25.3	2.16-21.66	0.35-3.85	Present study
Gulf of Aqaba[a]	0.8-3.5	-	0.55-1.9	Claessens *et al*. (2010)
Eastern Mediterranean[a]	0-0.78	-	-	Pitta and Giannakourou (2000)
E Subarctic Pacific[a]	3.4-28	-	-	Storm *et al*. (1993)
NW Indian Ocean[a]	0.03	-	-	Leakey *et al*. (1996)
Northern Arabian Sea, Gulf of Oman[a]	0.8	-	-	Leakey *et al*. (1996)
S California Coast[b]	0.5-45	-	-	Beers *et al*. (1980)
Kiel Bight[b]	Max. 92	-	-	Smetack (1981)
Southampton water[b]	-	1.0-9.0	7-10	Antai (1989)
Limfjord, Denmark[b]	-	0.1-4.2	1.3-3.4	Fenchel (1982)
Limfjord, Denmark[b]	-	0.2-15.2	0.5-15.2	Andersen and Sørensen (1986)
North Sea[a]	-	0.1-66	0.1-2.7	Nielsen and Richardson (1989)
Sargasso Sea[a]	-	0.2-1.1	0.2-0.9	Caron (1984)
Marine Snow, N Atlantic	-	1.3-182.0	0.9-252	Caron (1984)

[a] Open waters [b]Coastal waters

hypothesis might explain the unexpectedly high ciliate abundance in this ologotrophic marine habitat.

During the present study bacterial population densities at site (1) were recorded to vary between 1 x 10^6 ml^{-1} and $1.1x10^7$ ml^{-1}, which is much higher than those recorded at site (3), with values between 0.1 and $0.5x10^5$ ml^{-1} (Figure 4a). 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. As stated by Sanders *et al*.

Table 2. 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		
Bacteria	R.M.	N.	A.G.	R.M.	N.	A.G.
Bacteria numbers (L^{-1})	$11x10^9$	$5x10^9$	$5x10^9$	$1.0x10^9$	$0.5x10^9$	$1.0x10^9$
Flagellates						
TNAN numbers (L^{-1})	$3.15x10^7$	$2.52x10^7$	$1.43x10^7$	$0.41x10^7$	$0.22x10^7$	$0.051x10^7$
HNAN numbers (L^{-1})	$2.8x10^7$	$2.3x10^7$	$1.4x10^7$	$0.4x10^7$	$0.2x10^7$	$0.05x10^7$
Volume cleared/HNAN/hour* (L h^{-1})	10^{-8}	10^{-8}	10^{-8}	10^{-8}	10^{-8}	10^{-8}
Bacteria encountered/HNAN (h^{-1})	110	50	5	10	5	1
Volume cleared by HNANs in each litre in an hour (L)	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						
Filtering ciliate numbers (L^{-1})	33000	26000	17000	6000	300	20
Volume filtered/ciliates/hour** (L h^{-1})	$5x10^{-6}$	$5x10^{-6}$	$5x10^{-6}$	$5x10^{-6}$	$5x10^{-6}$	$5x10^{-6}$
Bacteria filtered/ciliate/hour (h^{-1})	55000	25000	2500	5000	2500	500
TNAN filtered/ciliate/hour (h^{-1})	157.5	126	71.5	20.5	11	2.55
Volume filtered by ciliates in each litre in one hour (L)	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	10000

(1992), 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) (Figure 4a), can be related to the decrease in chlorophyll *a* concentration, reflecting the more pronounced oligotrophy northward along the Gulf, as well as to food supply limitations and predation by heterotrophic flagellates at this site. Data in figure (5) supports the supposition that bottom-up control (food supply) is a more important factor in regulating bacterial abundance in this highly oligotrophic site than top-down control (predation). In other words, even in a situation where grazing pressure on bacteria at this protectorate (site 3) is reduced due to lower absolute abundances of hetereotrophic flagellates, the bacteria are not capable of rapid increases in abundance because of substrate limitations. This conclusion therefore supports that of Sanders *et al*. (1992) that in oligotrophic ecosystems the bacterial population is more strongly controlled by substrate supply.

It is interesting to compare the microbial loop population densities in the pelagic waters of the Gulf of Aqaba with those in the offshore waters, and also to compare those populations with those of more productive waters around the world. This comparison is illustrated from the data in table (1). Ciliate, heterotrophic flagellate and bacterial abundances in the water of the Gulf of Aqaba and in the water of other marine environments overlap strongly across most of the range of the oligotrophic-eutrophic continuum. The lowest abundances of these microorganisms, however, were observed in open water, as well as in oligotrophic habitats. Comparable maximum abundances were found in coastal waters or in more productive open ocean systems (Table 1). However, the highest abundances that have been observed in these open ocean systems can be compared to the highly eutrophic microzones of this aquatic environment (Caron *et al*., 1982, 1986).

Regarding the seasonal variations, the main peak of planktonic microbial abundance in the Gulf of Aqaba was recorded in spring, whereas summer harboured the lowest densities (Figure 6). The high abundances during the spring season seem to have been encouraged by the higher concentration of chlorophyll *a* and the more suitable water temperature during this season (Figure 6). As summer approaches, however, the surface habitat becomes more hostile due to the increasing temperature and the microbial density decreases. Moreover, during the summer, the recruitment into the Gulf of Aqaba diminishes due to the decreasing rate of water exchange towards the Red Sea through Bab El Mandab from the Indian Ocean.

The relationship between heterotrophic nanoflagellates and bacterial populations of these marine protectorates can be further illustrated from the data in table (2). Here it is shown that the number of bacteria that may be caught per flagellate per hour is 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 as being 27-254 bacteria/flagellate/hour and Sherr *et al*. (1983) found ingestion rates of 10-75 bacteria/flagellate/hour. Thus, the flagellate population of Ras Mohammed and Nabq protectorates could be able to maintain themselves with these ingestion rates of 10-110 bacteria/ flagellate/hour and 5-50 bacteria/flagellate/hour,

respectively. The flagellate populations of Abu Galoum protectorate, however, would surely not be able to maintain themselves with a very low year-round ingestion rate of just 1-5 bacteria/ flagellate/hour. It must be the case, therefore, that the heterotrophic nanoflagellates of this marine protectorate supplement bacteria with nanophytoplankton organisms as a food supply.

Pelagic food webs actually have a unique size dependency in feeding modes (Gaedke and Kamjunke, 2006). Filtration rates derived from the literature were used to calculate the potential rate of capture of prey of different categories of organism, as well as to estimate the time required for the whole water body to be filtered by hetrotrophic flagellates and filter feeding ciliates. The high populations of nanoflagellates filter the whole body of water every 3, 4 and 7 hours in spring at Ras Mohammed, Nabq and Abu Galoum protectorates respectively. On this basis, 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.

The ciliates could also be consuming bacteria, but flagellates are a more likely food source, and presumably a more "attractive" one for ciliates in view 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 waters of the Ras Mohammed protectorate are numerous enough during spring to filter the whole water body four times a day, and the ciliate population could therefore surely 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 gives less opportunity for growth. It is conceivable that the balance must depend on the relative sizes of the organisms involved (Rassoulzadegan *et al*., 1988).

In conclusion, the Gulf of Aqaba is regarded 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, ciliate density was, however, astonishingly high. Abundances were at times eight-fold higher than those found in comparable studies on nutrient-poor pelagic systems and approached those observed in coastal waters, indicating that the ciliates were highly efficient in utilizing the available food in the gulf protectorates, and suggesting that the planktonic food web in this oligotrophic habitat is dominated by the microbial loop. 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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