



## Original article

## Complex interactions and different possible pathways among functional components of the aquatic microbial world in Farasan Archipelago, Southern Red Sea, Saudi Arabia

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## ABSTRACT

This work aims to outline the dynamics of trophic links between the three main microbial components (bacteria, nanoflagellates, and ciliates) of the Farasan Archipelago in order to establish a baseline for future research in this area. The Farasan Archipelago lies along the southwestern coast of the Saudi Arabia, southern Red Sea between 16°20'–17°10'N and 41°30'–42°30'E and had been declared as marine and terrestrial reserve by the year 1996. Three different sites were chosen for this study, with each site visited bimonthly for 18 months from September 2016 to February 2018. Bacteria, nanoflagellates and ciliates were enumerated in order to explore the complex interactions between the main microbial categories in sea waters of the Farasan Archipelago. High abundances were recorded during the present study for bacteria ( $8.7 \times 10^6$  bacteria ml<sup>-1</sup>), nanoflagellates ( $3.7 \times 10^4$  TNAN ml<sup>-1</sup>) and ciliates (40.4 ciliates ml<sup>-1</sup>). The paper discusses the various potential pathways controlling the complex interactions between these microbial groups in this part of the southern Red Sea. It is concluded that a linear trophic chain consisting of bacteria; heterotrophic nanoflagellates; filter feeding ciliates is a major route by which the production of bacteria is transferred to the higher consuming levels, thereby confirming the high importance of bottom-up control (food supply), alongside top-down control (predation) in regulating bacterial abundances in the Farasan Archipelago. During the present investigation, each nanoflagellate ingested between 11 and 87 bacteria in one hour, while each ciliate consumed between 20 and 185 nanoflagellates every hour. These calculated grazing rates of protistan eukaryotes confirmed the role of heterotrophic nanoflagellates as the main consumers of bacteria, and the role of ciliates as the major control for the heterotrophic nanoflagellate population dynamics, and thus the top predators within the microbial plankton assemblage in the Farasan Archipelago.

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## 1. Introduction

Sea water contains a very wide range of microorganisms; some of them are belonging to the most primitive, while others belonging to the most advanced branches of the tree of life. It is now well

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known that every liter of clear blue water is teeming with a huge number (~billions) of microbial organisms in the form of bacteria, archaea, viruses, protists and fungi, far exceeding all multicellular metazoans in their abundance and diversity. Over the last four decades, extensive research has revealed the crucial roles of microbial organisms in aquatic and terrestrial ecosystems, because they are a large fraction of the biomass with relatively high metabolic rates, and actually dominating the flux of energy between trophic levels as well as providing all-important biochemical elements in these ecosystems (Pomeroy, 1980; Azam et al., 1983; Fuhrman and Suttle, 1993; Pernthaler, 2005; Esteban et al., 2006; Pedros-Alio, 2006; Foissner, 2016; Abraham et al., 2019).

The frequent interactions among these microbiological compartments in the sea water are responsible for strong trophic links

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through two main mechanisms: 1- microbial loop (Azam et al., 1983), in which bacteria represent the foundation of microbial food webs in aquatic ecosystems, and 2- viral shunt (Bratbak et al., 1992), in which viruses are the effective players in the mortality of microbial organisms and disease for higher organisms and strongly interact with the geochemical cycling (Suttle, 2005, 2007). Hence, strong selection pressures on each functional biotic compartment will be developed in the ecosystem and diversified nature of these interactions contribute to maintaining high biodiversity in the aquatic ecosystem (Breitbart et al., 2002; Venter et al., 2004). This means that each component of these functional groups, with particular reference to bacteria, viruses and protistan grazers, is likely to have a major impact on the structure of the community itself, as well as a further impact on the biological and chemical functions of each other group as a direct result of these diversified interactions.

The present work aims to focus on the interaction between three major players in the microbial world of the Farasan Archipelago: a- heterotrophic bacteria, b- nanoflagellates and c- filter feeding ciliates, to explore the complex interactions among the black boxes of prokaryotes (bacteria) and eukaryote protistan grazers (nanoflagellates and filter feeding ciliates) so as to establish a baseline for further studies in the future.

## 2. Material and methods

### 2.1. The study area

The Red Sea (2250, 355 km and 490 m for maximum length, maximum width and average depth, respectively) is a long narrow

sea separating northeast Africa from the Peninsula of Arabs. It shows several features which are unique among tropical oceans: (1) it is blocked by land from the north and has no river inflow; (2) rainfall is extremely scant and restricted to a few months of the year; (3) its isothermal subsurface water has high salinity of 40.5 ‰ (Halim, 1984), and warm temperature of 21.7 °C (Morcos, 1970); (4) it has low nutrient concentrations, low primary production ( $100 \text{ mg C m}^{-2} \text{ d}^{-1}$ ) and high true phytoplankton production ( $<1 \text{ g C m}^{-2} \text{ d}^{-1}$ ) (Shaikh et al., 1988).

The Farasan Archipelago lies in the southern part of the Red Sea between  $16^{\circ}20' - 17^{\circ}10' \text{N}$  and  $41^{\circ}30' - 42^{\circ}30' \text{E}$  (Fig. 1), and was declared as protected area in 1996 (NCWCD, 2000). It lies approximately 50 km from the coastal town of Jizan in southern Saudi Arabia, and comprises many (~90) islands of various sizes (ranging from 381 km<sup>2</sup> for the biggest island “Farasan Alkhubra” to a few square meters for the small islets) (BACP, 1997). The largest islands, “Farasan Alkhubra” and “As Saqud” are the only permanently inhabited ones. The archipelago contains several unique plants, mangroves (red & black), and other endemic invertebrate and vertebrate organisms, as well as breeding colonies of many sea birds and sea turtles (Thouless, 1991). It has significant fish stocks but, unfortunately, overfishing is a major threat (Kingdon, 1990; Masseti, 2010).

### 3. Sampling and laboratory techniques

A total of 243 water samples were collected from three different sites within the archipelago (Fig. 1). The locations and various details for each of the three sampling sites are presented in Table 1. Sampling was conducted nine times, roughly every two months

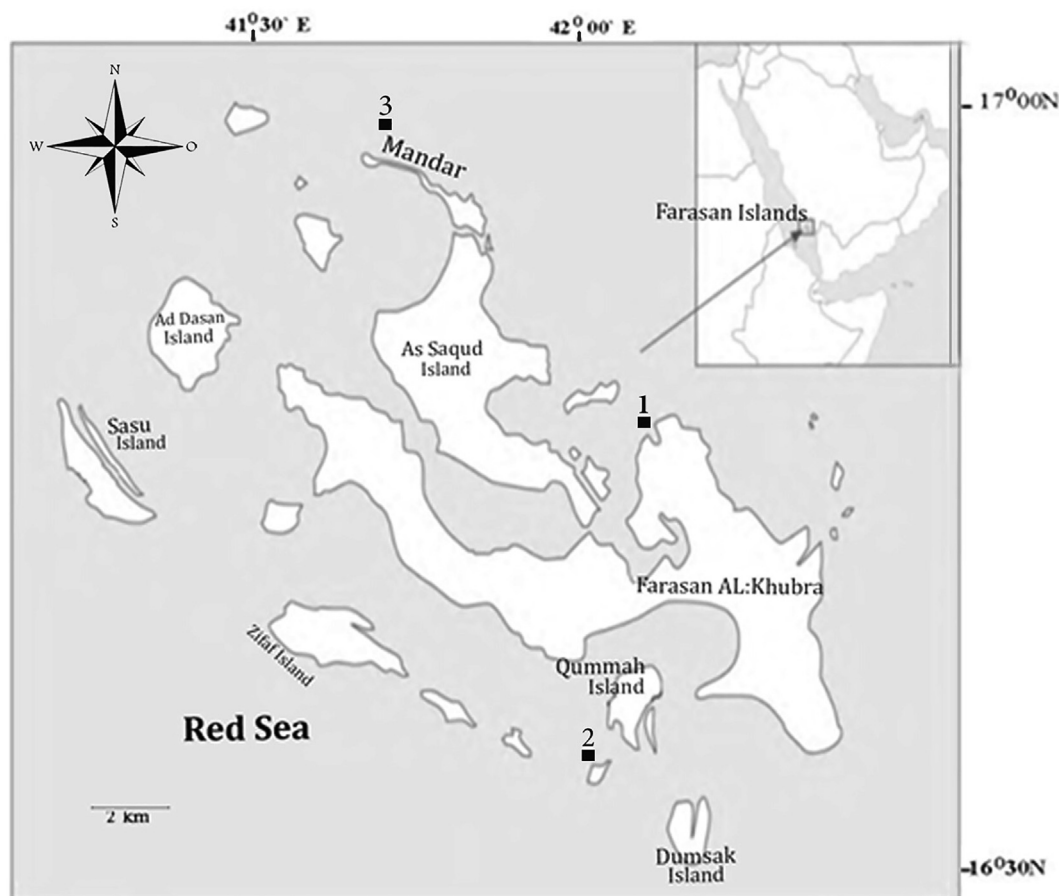


Fig. 1. The geographical location of the sampling stations at Farasan archipelago in the Southern Red Sea.

**Table 1**  
Sampled localities with their GPS coordinates and biota recorded during the present study.

Sampling sites	Coordinates of sampling sites	General features and dominant fauna and flora
(Site 1)	16° 47' 19.8"N–42° 06' 15.8"E	-Sandy silt substrate - <b>Flora:</b> <i>Rhizophora mucronata</i> (Mangroves); <i>Halophila ovalis</i> , (Seagrasses); <i>Padina</i> sp.(Algae). - <b>Fauna:</b> <i>Cassiopeia andromeda</i> (Cnidarians); <i>Littorina scabra</i> , <i>Cerithidea cingulate</i> , <i>Cassidula</i> sp., <i>Saccostrea cucullata</i> (Molluscs); <i>Metopograpsus messor</i> , <i>Macrophthalmus depressus</i> , <i>Uca inversa</i> (Crustaceans); High abundance of fish.
(Site 2)	16° 33' 10"N- 42° 03' 57.2"E	-Silty mud substrate - <b>Flora:</b> <i>Avicennia marina</i> (Mangroves); <i>Halophila ovalis</i> , <i>H. stipulacea</i> ; <i>Thalassia hemprichii</i> , <i>Thalassodendron ciliatum</i> (Seagrasses); <i>Padina</i> sp., <i>Enteromorpha</i> sp., <i>Sargassum</i> sp. (Algae). - <b>Fauna:</b> <i>Aurelia</i> sp., <i>Cassiopeia andromeda</i> (Cnidarians); <i>Littorina scabra</i> , <i>Cerithidea cingulate</i> , <i>Cassidula</i> sp., <i>Saccostrea cucullata</i> (Molluscs); <i>Dotilla sulcate</i> , <i>Metopograpsus messor</i> , <i>Macrophthalmus depressus</i> <i>Uca inversa</i> , <i>U. lacteal albimana</i> , <i>U. urvillei</i> (Crustaceans).
(Site 3)	16° 57' 59.5"N- 41° 40' 04.5"E	-Silt/reef rock substrate - <b>Flora:</b> <i>Halophila ovalis</i> , (Seagrasses); <i>Padina</i> sp. (Algae). - <b>Fauna:</b> <i>Cassiopeia andromeda</i> (Cnidarians); <i>Littorina scabra</i> , <i>Cerithidea cingulate</i> , <i>Cassidula</i> sp., <i>Saccostrea cucullata</i> , <i>Nerita albicilla</i> (Molluscs); <i>Metopograpsus messor</i> , <i>Macrophthalmus depressus</i> , <i>Uca inversa</i> (Crustaceans).

during the period from September 2016 to February 2018. During sampling, the water temperature was recorded using mercury in glass thermometer calibrated to 0.1 °C. The water salinity was periodically cross-checked with a hand-held AO/TC refractometer. A pre-calibrated digital pH meter was used to record the pH. Dissolved oxygen in the water samples was determined using the standard macro-Winkler method (Parsons et al., 1984). On each visit, nine separate samples of 500 ml each were collected from a depth of about 50 cm within each site using glass jars closed by plastic tops, and of these three were used for measuring the concentration of chlorophyll *a* using the acetone extract method (Golterman, 1969); another three samples were used for determination of the dissolved oxygen content using the standard macro-Winkler method (Parsons et al., 1984), the last three samples were used for enumeration of the microbial organisms: heterotrophic bacteria, nanoflagellates and ciliates. Ciliates were counted in three Lugol-fixed (1% final concentration (Thronsdon, 1978)) subsamples (of 100 ml each) under an inverted phase contrast microscope (Wild M40) at a magnification of 400× using the Utermöhl

(1958) method. Bacteria and nanoflagellates were counted in three glutaraldehyde fixed subsamples (of 10 ml each) after staining with DAPI stain using an epifluorescence microscope (Olympus BX5) at a magnification of 1000× according to Porter and Feig (1980).

#### 4. Results

Most physicochemical conditions differed across the three different sites within the Farasan Archipelago (Table 2), although these variations were not the same. Near surface water temperature showed the lowest values of 17.2 °C during winter at site 2, accompanied with low water salinity of 35 ‰. pH values ranged from 8.1 to 8.31, reflecting the slightly alkaline nature of the water in the Farasan Archipelago. Low concentrations of chlorophyll *a* were recorded (0.01–0.9 µg ml<sup>-1</sup>) during the present study. The highest chlorophyll *a* concentration of 0.9 µg ml<sup>-1</sup> was recorded at site 2 and coinciding with the highest dissolved oxygen contents of 6.9 mg l<sup>-1</sup>.

**Table 2**  
Averages and ranges of environmental and biological parameters for the three sampling sites.

Parameter	Sites					
	Site 1		Site 2		Site 3	
	Mean	Range	Mean	Range	Mean	Range
Temperature (°C)	26.22 ± 3.0	18.7–35.6	25 ± 2.7	17.2–33.8	24.6 ± 3.3	20.4–35.2
Salinity (‰)	35.40 ± 2.1	35.6–38.7	34.8 ± 1.8	35.0–38.8	34.7 ± 2.2	36.2–39.4
pH	8.01 ± 0.01	8.1–8.24	8.01 ± 0.01	8.12–8.27	7.9 ± 0.10	8.11–8.31
Dissolved Oxygen (mg l <sup>-1</sup> )	4.60 ± 1.3	5.4–6.3	5.8 ± 1.5	5.7–6.9	5.4 ± 1.20	5.5–6.4
Chlorophyll <i>a</i> (µg ml <sup>-1</sup> )	0.11 ± 0.01	0.1–0.3	0.52 ± 0.0	0.4–0.9	0.6 ± 0.12	0.01–0.2
Bacteria (× 10 <sup>6</sup> ml <sup>-1</sup> )	1.31 ± 0.9	0.8–2.4	6.6 ± 1.4	1.1–8.7	0.96 ± 0.2	1.7–1.9
Total Nanoflagellates (× 10 <sup>4</sup> ml <sup>-1</sup> )	1.20 ± 0.04	0.5–2.7	2.4 ± 1.1	0.89–3.7	0.76 ± 0.2	0.4–1.9
Heterotrophic Nanoflagellates (× 10 <sup>4</sup> ml <sup>-1</sup> )	1.41 ± 0.6	0.4–2.4	2.2 ± 0.8	0.8–3.2	0.8 ± 0.13	0.2–1.6
Ciliates (ml <sup>-1</sup> )	27.13 ± 4.1	24.8–33.5	33.4 ± 5.7	29.2–40.4	12.3 ± 2.1	10.6–15.4

The average cell numbers recorded for heterotrophic bacteria, auto and heterotrophic nanoflagellates and filter feeding ciliates are given in Table 2. Abundances of these microbial groups were high during spring and low in summer, also site number two sustained the highest abundances while site number three contained the lowest microbial population densities. Bacterial abundances in the surface water of the Farasan Archipelago varied between  $0.7 \times 10^6 \text{ ml}^{-1}$  at site 3 and  $8.7 \times 10^6 \text{ ml}^{-1}$  at site 2. There was a higher abundance of total nanoflagellates at site 2 ( $3.7 \times 10^4 \text{ ml}^{-1}$ ) compared to site 3 with just  $0.4 \times 10^4 \text{ ml}^{-1}$ . Ciliates abundance ranged from 10.6 cells  $\text{ml}^{-1}$  in the waters of site 3 to 40.4 cells  $\text{ml}^{-1}$  at site 2.

Table 3 compares the microbial densities in the oligotrophic water of the Farasan Archipelago and those of more productive waters worldwide. A comparison between the filtration activities of the heterotrophic flagellates and filter feeding ciliates during spring and summer seasons is shown in Table 4. Possible mathematical interactions and pathways among the main compartments of the microbial world of the Farasan Archipelago are summarised in the Fig. 2.

## 5. Discussion

The purpose of this work was to examine the interactions and possible pathways between bacteria, as food supply, and their primary eukaryotic consumers in the aquatic ecosystem of the Farasan Archipelago. The study revealed a high abundance of bacteria in this oligotrophic habitat with values ranging from 0.7 to  $3.7 \times 10^6$  bacteria  $\text{ml}^{-1}$  (Table 2). A number of studies have indicated that bacterial abundance increases with trophic state and is positively correlated to chlorophyll *a* concentration (Azam et al., 1983; White et al., 1991). In the aquatic ecosystem of the Farasan Archipelago, however, oligotrophic conditions and low chlorophyll *a* concentration ( $0.01\text{--}0.9 \mu\text{g ml}^{-1}$ ) coincide with high bacterial population density. This might suggest that terrestrial influences supplement marine production in supplying the aquatic ecosystem with nutrients. This hypothesis is supported by so explicitly of the presence of terrestrial organic materials (leaves, twigs and foods) in the water of the archipelago.

Moreover, the high bacterial abundance recorded during the present study was also accompanied by a high abundance of other members of the microbial community *i. e.* nanoflagellates and

**Table 3**

Ranges of ciliates, flagellates and bacterial population density of the oligotrophic Farasan Archipelago in comparison with those of more productive open (a) and coastal (b) water worldwide.

Location	Ciliates number ( $\times 10^3$ cells $\text{L}^{-1}$ )	Flagellates number ( $\times 10^3$ cells $\text{ml}^{-1}$ )	Bacteria number ( $\times 10^6$ cells $\text{ml}^{-1}$ )	Source
Farasan Archipelago	10.6–40.4	4–37	0.8–8.7	Present study
Gulf of Aqaba <sup>a</sup>	0.8–3.5	–	0.55–1.9	Claessens et al. (2010)
Eastern Mediterranean <sup>a</sup>	0–0.78	–	–	Pitta and Giannakourou (2000)
E Subarctic Pacifica	3.4–28	–	–	Strom et al. (1993)
NW Indian Ocean <sup>a</sup>	0.03	–	–	Leakey et al. (1996)
S California Coast <sup>b</sup>	0.5–45	–	–	Beers et al. (1980)
Kiel Bight <sup>b</sup>	23–92	–	–	Smetacek (1981)
Southampton water <sup>b</sup>	–	1.0–9.0	7–10	Antai (1989)
Limfjord, Denmark <sup>b</sup>	–	0.1–4.2	1.3–3.4	Fenchel (1982)
Limfjord, Denmark <sup>b</sup>	–	0.2–15.2	0.5–15.2	Andersen and Sørensen (1986)
North Sea <sup>a</sup>	–	0.1–66	0.1–2.7	Nielsen and Richardson (1989)
Sargasso Sea <sup>a</sup>	–	0.2–1.1	0.2–0.9	Caron (1984)
Marine Snow, N Atlantic	–	1.3–182.0	0.9–252	Caron (1984)

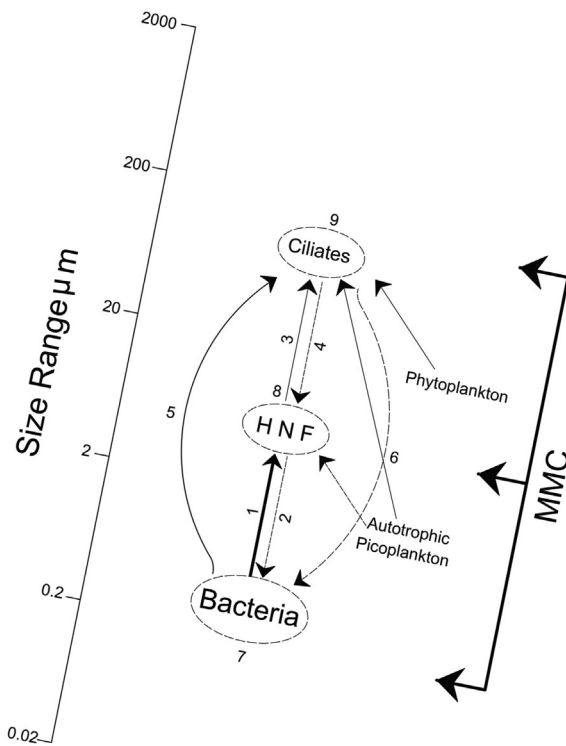
**Table 4**

Estimates of the clearance rates and potential rates of food capture by protistan grazers during spring and summer 2017 at the three sites of the Farasan Archipelago.

	Spring 2017			Summer 2017		
	Site 1	Site 2	Site 3	Site 1	Site 2	Site 3
<b>Bacteria</b>						
Bacterial density ( $\text{L}^{-1}$ )	$2.4 \times 10^9$	$8.7 \times 10^9$	$1.9 \times 10^9$	$0.8 \times 10^9$	$1.1 \times 10^9$	$1.7 \times 10^9$
<b>Flagellates</b>						
TNFs number ( $\text{L}^{-1}$ )	$2.7 \times 10^7$	$3.7 \times 10^7$	$1.9 \times 10^7$	$0.5 \times 10^7$	$0.89 \times 10^7$	$0.4 \times 10^7$
HNFs number ( $\text{L}^{-1}$ )	$2.4 \times 10^7$	$3.2 \times 10^7$	$1.6 \times 10^7$	$0.4 \times 10^7$	$0.8 \times 10^7$	$0.2 \times 10^7$
Volume cleared/HNF/hour* ( $\text{L h}^{-1}$ )	$10^{-8}$	$10^{-8}$	$10^{-8}$	$10^{-8}$	$10^{-8}$	$10^{-8}$
Bacteria encountered/HNF ( $\text{h}^{-1}$ )	24	87	19	8	11	17
Volume cleared by HNFs in each litre in an hour (L)	0.24	0.32	0.16	0.04	0.08	0.04
Time for HNFs to filter whole water body (h)	4	3	6	25	12.5	25
<b>Ciliates</b>						
Ciliates number ( $\times 10^3 \text{ L}^{-1}$ )	33.5	40.4	15.4	24.8	29.2	10.6
Volume filtered/ciliate/hour** ( $\text{L h}^{-1}$ )	$5 \times 10^{-6}$	$5 \times 10^{-6}$	$5 \times 10^{-6}$	$5 \times 10^{-6}$	$5 \times 10^{-6}$	$5 \times 10^{-6}$
Bacteria filtered/ciliate/hour ( $\times 10^3 \text{ h}^{-1}$ )	12	44	10	40	6	9
TNFs filtered/ciliate/hour ( $\text{h}^{-1}$ )	135	185	95	25	44.5	20
Volume filtered by ciliates in each litre in an hour (L)	0.1675	0.202	0.077	0.124	0.146	0.053
Time for ciliates to filter whole water body (h)	6	5	13	8	7	19

\* Mean value from Fenchel (1982).

\*\* Mean value for loricate and non-loricate ciliates from Heinbokel (1978), Heinbokel and Beers (1979), Verity (1987), Jonsson (1986), Sherr et al. (1986).



**Fig. 2.** The mathematically nine different possible pathways showing complex interactions between bacteria, nanoflagellates and filter feeding ciliates. 1,2 = the trophic interactions between bacteria and heterotrophic nanoflagellates (HNFs); 3, 4 = the trophic interaction between HNFs and filter feeding ciliates; 5,6 = the trophic interactions between heterotrophic bacteria and ciliates; 7, 8, 9 = interspecies interaction (cannibalism) within each functional group of bacteria, heterotrophic nanoflagellates and filter feeding ciliates, respectively. MMC = Microbial mortality causatives.

ciliates, with particular reference to site 2 (Table 2). It is known that mangroves provide a unique environmental niche for a wide range of microbial organisms (Sahoo and Dhal, 2009) and, in this study, the flourishing mangal ecosystem at site 2 with its huge *Avicennia marina* mangrove trees, seemed to have a direct impact on the abundance of prokaryotes and eukaryotes, probably as a result of the large amount of detritus substances with their associated nutrients in these mangroves aquatic habitats. The high population densities characterising the microbial communities of the Farasan Archipelago decreased during the hot summer months, probably because the surface water habitat then becomes more hostile with the increasing temperature. Moreover, the decreasing water exchange rate towards the Red Sea from the Indian Ocean through Bab El Mandab (Halim, 1984) actually diminishes the recruitment into the Farasan Archipelago water during the summer, and thence the microbial density decreases.

Grazing, as well as clearance rates of heterotrophic nanoflagellates and ciliates, has been calculated on simplified mathematical assumptions (Table 4). The uptake rates calculated from this study revealed values ranging between 8 and 87 bacteria consumed by heterotrophic flagellate in one hour are well within range of published data elsewhere (10–80 bacteria  $\text{HNF}^{-1} \text{h}^{-1}$  and which has been reviewed by Sherr et al., 1986). One would be justified, therefore, to conclude that heterotrophic nanoflagellates in the Farasan Archipelago can thrive solely on a bacterial diet, especially during spring, but that other food sources, such as autotrophic picoplankton (Fig. 2) have to be considered and/or supposed for heterotrophic nanoflagellates, especially during the hot summer months.

The data presented in Table 4 and summarised in Fig. 2, clearly confirms that, in the Farasan Archipelago, heterotrophic nanoflagellates are the main bacterial consumer, however, ciliates could also be consuming bacteria and nanoflagellates. This suggests that nanoflagellates can be considered as the “missing link” in ciliate-bacterial interactions. Moreover, they are a more likely food source, and presumably a more “attractive” one for ciliates, for two main reasons: 1- the much greater nutritive value of each nanoflagellate cell, and 2- the bigger size of flagellate cells is more suited to the coarser filter required by ciliates (Fenchel, 1988; El-Serehy and Sleight, 1993; First and Hollibaugh, 2010). It is also bearing in mind that several ciliate species are well known as carnivores (Weisse, 1989; Weisse and Müller, 1990). Thus, group-cannibalism occurs among the ciliate community, and the same holds true for the heterotrophic nanoflagellates and bacterial assemblages of the Farasan Archipelago. Thus ciliates are important bacterial and/or nanoflagellate consumers and are the top predators within these microbial planktonic assemblages, with ingestion rates varying between 6 and  $44 \times 10^3$  bacteria  $\text{CIL}^{-1} \text{h}^{-1}$  and  $0.2\text{--}1.85 \times 10^2$  flagellate  $\text{CIL}^{-1} \text{h}^{-1}$ . It can therefore be concluded that ciliates largely control heterotrophic nanoflagellates abundances and partially control bacterial population dynamics in the Farasan Archipelago throughout most of the year.

It is clear from the large population numbers of prokaryotes (bacteria) and eukaryotes (nanoflagellates and ciliates) that the water column within Farasan Archipelago is especially productive during spring, where the high population density of nanoflagellates can filter the whole water body six times a day. This clearly requires a very quick reproduction rate for the bacterial population and/or a continuous very active recruitment of bacterial communities into this habitat. Moreover, the filter feeding ciliate population is also numerous enough during this season (spring) to filter the whole water body three times a day, and the population of ciliates could therefore surely catch enough flagellates during this time to help in reducing the intense grazing pressure on bacteria by the flagellates, giving the former a chance to reproduce and/or be recruited.

In conclusion, this study presents the first investigation for the microbial world in the Farasan Archipelago in the southern Red Sea. The results demonstrate that the archipelago water column is particularly productive in spring, and that the various environments within the archipelago are inhabited by highly active microbial communities including: bacteria, nanoflagellates and filter feeding ciliates, with the presence of high population densities of prokaryotes (bacteria) as the principal food supply and an abundance of eukaryotes (flagellates and ciliates) as active grazers. Bacterial abundances were high in this Red Sea oligotrophic habitat, confirming bottom-up control (food supply) as the dominant component of the microbial loop in this habitat, although predation by heterotrophic nanoflagellates and filter feeding ciliates is also very important in controlling bacteria (domination of top-down control). Within the microbial loop dominating the Farasan Archipelago, a linear food chain consisting of bacteria-heterotrophic nanoflagellates-filter feeding ciliates is a potential major route transferring the production of bacteria to higher consuming levels of the planktonic assembly. Future research, however, needs to determine whether microbial mortality players (i.e. viruses) participate alongside the eukaryotic flagellate and ciliate grazers in controlling the bacterial population dynamics in the Farasan Archipelago.

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