



Note

Bacterial and zooplankton distribution in deep waters of the Arabian Sea

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Abstract

The distribution of free-living bacteria and mesozooplankton was investigated at two deep sites (~4000 m) in the western (WAST) and central (CAST) Arabian Sea in February 1998 during the late NE monsoon. In the epipelagic zone (0–150 m), biomass expressed as carbon was lower in bacteria (WAST: 3.31–0.93 mg C m⁻³, CAST: 2.00–1.32 mg C m⁻³) as compared to mesozooplankton (WAST: 11.39–3.32 mg C m⁻³, CAST: 9.83–1.84 mg C m⁻³). In the core of the oxygen minimum zone (150–400 m), mesozooplankton biomass abundance (WAST: 0.26 mg C m⁻³, CAST: 0.08 mg C m⁻³) decreased sharply whereas bacterial biomass increased from minima of 0.28 mg C m⁻³ and 1.32 mg C m⁻³ to 0.75 mg C m⁻³ and 12.42 mg C m⁻³ at WAST and CAST, respectively. At greater depths (>400 m), mesozooplankton biomass was elevated in oxygenated waters, but decreased more distinctly from 0.53 mg C m⁻³ at WAST and 0.42 mg C m⁻³ at CAST to 0.02 mg C m⁻³ (WAST and CAST at 50 m above bottom) than bacteria, which varied between 1.18–1.56 mg C m⁻³ at WAST and 0.53–1.13 mg C m⁻³ at CAST below 700 m. This results in a high relative abundance of bacteria in the bathypelagic zone (>1000 m). A comparison of bacterial cell numbers compiled from different sources and seas shows that, in general, the decrease in abundance with depth is low below 600–800 m. Irrespective of the ocean region, the abundance ranged within one order of magnitude, with lowest values at oligotrophic sites and highest values at eutrophic sites.

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1. Introduction

Carbon dioxide is transformed into organic carbon via photosynthetic activity by phytoplankton in the euphotic zone of the oceans. Phytoplankton is consumed by herbivorous organisms

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that are fed upon by omnivorous and carnivorous animals. Ungrazed cells, viral lysis, transparent exopolymer particles (TEP), carcasses and fecal material produce particulate organic carbon (POC). This material is eaten by detritivorous zooplankton, is remineralized by bacterial activity, or sinks to greater depths. POC is partly transformed into dissolved organic carbon (DOC) by metabolic activity and fuels the microbial loop (see Williams, 1990; Ducklow, 2000).

Information on the vertical distribution of free-living bacteria and their contribution to carbon flux to bathypelagic depths is sparse (see Nagata et al., 2000; Hansell and Ducklow, 2003), as are papers that deal with comparisons of bacterial distributions and other planktonic groups to describe interactions of the biota in the ocean's interior. Patterson et al. (1993) and Tanaka and Rassoulzadegan (2002) investigated the distribution of bacteria and protozoa down to bathypelagic depths of the NE Atlantic and the NW Mediterranean, respectively, and Raghukumar et al. (2001) did so in the Arabian Sea. Yamaguchi et al. (2002) investigated concomitantly the deep distribution of bacterio-, phyto-, protozoo- and metazooplankton. Their study was done at sites of different productivity in the Pacific Ocean. Knowledge about the abundance and vertical distribution of functional groups within the plankton community will give insights into their contribution to carbon utilization in the sea.

Our paper will describe the vertical distribution of free-living bacteria and zooplankton at two deep sites in the Arabian Sea. We will show that bacterial biomass is higher than mesozooplankton biomass in the deep-sea and that the vertical distribution of bacteria and mesozooplankton is influenced by a very pronounced zone of permanent oxygen deficiency between the lower boundary of the euphotic zone and more than 1000 m depth that extends over large areas of the Arabian Sea (Sewell and Fage, 1948; Olson et al., 1993).

2. Material and methods

Water bottle and net samples were taken at two sites in the Arabian Sea (Fig. 1) to determine the

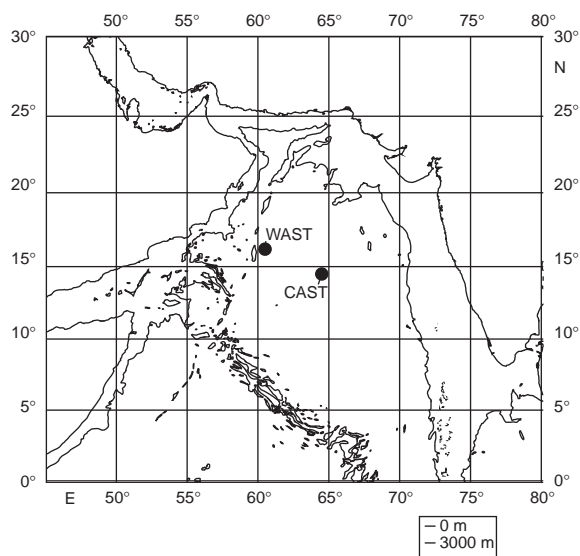


Fig. 1. Sampling sites in the Arabian Sea.

abundance and distribution of bacteria and mesozooplankton during Sonne cruise 129 (Pfannkuche and Utecht, 1999): at the Western and Central Arabian Sea Sediment Trap stations WAST ($16^{\circ}15'N$, $60^{\circ}20'E$, water depth 4050 m) and CAST ($14^{\circ}30'N$, $64^{\circ}30'E$, water depth 3950 m). Samples were taken at the end of the NE monsoon, when enhanced production in the northern part of the basin occurs (Sarangi et al., 2001).

Water was sampled at discrete depths of 20, 60, 100, 200, 300, 500, 700, 1500, 2500 and 3550 m (only WAST) at WAST on 4/5 February 1998 during the night and at CAST on 24 February 1998 during the day, with a Seabird CTD (SBE 911) equipped with 101 Niskin bottles. Concomitantly, salinity, temperature ($^{\circ}C$) and oxygen ($\mu\text{mol O}_2\text{l}^{-1}$) profiles were obtained. Samples for the analysis of bacteria were preserved with formaldehyde buffered with sodium tetraborate at a concentration of 4%. The water samples were stored under dark and cold conditions and were counted within 3–4 months after sampling. Turley and Hughes (1994) and Gundersen et al. (1996) stated that bacteria counts decline with prolonged storage. The storage time may have reduced the number of bacteria in our samples by 50%. However, as indicated in Fig. 2, a bacterial

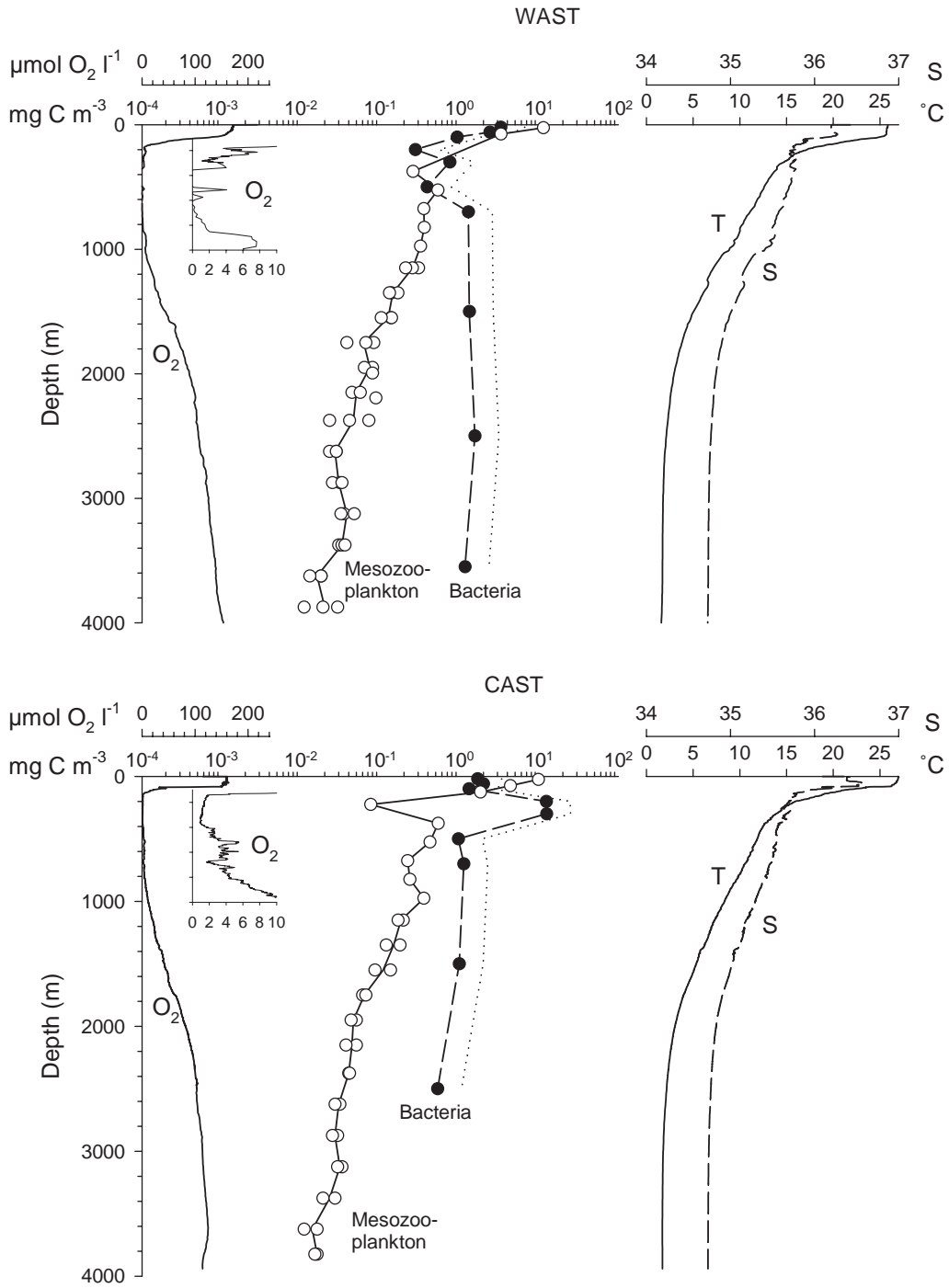


Fig. 2. Bacterial and mesozooplankton biomass in relation to oxygen content, temperature and salinity distribution at WAST and CAST in the Arabian Sea. Mesozooplankton mean data (solid line) and single data points are indicated. The dotted line indicates the potential bacterial biomass during sampling assuming a loss in bacterial numbers of 50% due to storage (see Section 4).

biomass higher by a factor of 2 will not affect the general conclusion of this study. To determine the abundance of bacteria, 5×20 ml subsamples were stained with DAPI (4,6 diamidino-2-phenylindole) at a concentration of $1 \mu\text{g}$ DAPI per 1 ml water (Porter and Feig, 1980), filtered onto $0.2 \mu\text{m}$ black Nuclepore filters and inspected with an epifluorescence microscope. A total of 200 bacteria was counted on each filter. The biomass of bacteria expressed as carbon was calculated by assuming a carbon content of $15 \times 10^{-15} \text{g cell}^{-1}$ (Caron et al., 1995; Fukuda et al., 1998).

Mesozooplankton was collected with a 1m^2 Double MOCNESS (Multiple opening/closing net and environmental sensing system; Wiebe et al., 1985) at WAST between 2 and 7 February 1998 and at CAST between 19 and 27 February 1998. The device was equipped with 18 black nets of $333 \mu\text{m}$ and 2 nets of $100 \mu\text{m}$ mesh size. Three and two profiles below 1050 m were taken at WAST and CAST, respectively, and one profile for the upper 1050 m at each station. Although only one profile was taken at each station in the upper 1050 m, a large volume of 3265m^3 at WAST and 3042m^3 at CAST was filtered. The MOCNESS integrates over patchy distribution of meter scales, so that the catch will not be affected by small-scale variability. This study reports on the $333 \mu\text{m}$ mesh samples. Oblique sampling at finely spaced depth intervals was carried out at a speed of about 2 knots commencing as deep as 50 m above bottom (mab). Sampling details are given by Koppelman et al. (2003) and Pfannkuche and Utecht (1999). The samples were fixed in a 4% formaldehyde-seawater solution buffered with sodium tetraborate. On land, the material was fractionated through a set of sieves resulting in fractions of >5 , 5–2, 2–1, 1–0.5 and <0.5 mm, wet weighed according to the method of Tranter (1962) and counted. This study reports on the sum of fractions <5 mm; data on the fractionated material are given by Koppelman et al. (2003). Carcasses and exoskeletons, discriminated according to Weikert (1977), were counted separately. Most of the gelatinous plankton belonged to the sieve fraction >5 mm which is not treated in this study. In the upper 1000 m only night data are presented. Below 1000 m, where diel vertical migrations are negligible (Angel et al.,

Table 1

Carbon content (weight % of wet weight) for different sieve fractions of mesozooplankton in different depth zones in the Arabian Sea

Depth (m)	<0.5 mm	0.5–1 mm	1–2 mm	2–5 mm
0–300	4.5	4.8	5.0	4.3
300–450	4.0	5.6	4.8	4.3
450–1050	4.4	5.2	5.7	5.0
1050–1250	3.2	5.0	4.8	4.8
1250–1450	3.2	4.9	4.7	4.7
1450–1650	2.4	4.7	4.9	5.0
1650–2050	2.3	4.5	4.7	4.7
2050–2250	2.4	3.8	5.2	4.3
2250–2500	2.3	3.7	4.9	4.1
2500–2750	2.0	3.5	4.2	4.5
2750–3000	2.3	4.0	4.9	5.1
3000–3250	2.2	3.9	4.7	4.3
3250–3500	2.1	3.8	4.5	4.1
3500–3750	1.4	1.4	4.2	2.8
3750–3900	1.6	1.6	4.9	3.3

1982), day and night samples were averaged. The wet weights were converted into carbon with conversion factors obtained by carbon measurements of zooplankton samples from different depth zones in the open Arabian Sea (Table 1).

3. Results

3.1. Abiotic parameters

Temperature, salinity and oxygen content (Fig. 2) were highest in the upper 50 m of the water column at WAST ($T = 25.9^\circ\text{C}$, $S = 36.3$ – 36.4 , $\text{O}_2 = 170 \mu\text{mol l}^{-1}$) and CAST ($T = 26.8$ – 26.9°C , $S = 36.4$ – 36.5 , $\text{O}_2 = 153$ – $163 \mu\text{mol O}_2 \text{l}^{-1}$). Between 50 and 200 m all parameters decreased sharply. Below 170 m at WAST and 130 m at CAST, a marked oxygen minimum zone (OMZ) extended to 930 m at WAST and 850 m at CAST, with concentrations of less than $6 \mu\text{mol O}_2 \text{l}^{-1}$. At greater depths, the increase of oxygen to $153 \mu\text{mol O}_2 \text{l}^{-1}$ at 4000 m at WAST was not completely paralleled at CAST. Here, oxygen increased to $125 \mu\text{mol O}_2 \text{l}^{-1}$ at 3600 m, but below this depth it slightly decreased to $116 \mu\text{mol O}_2 \text{l}^{-1}$

at 3940 m. Temperature and salinity declined at a lower, but nearly linear, rate with depth below the thermocline from 200 to 2000 m. Below 2500 m, these parameters were nearly constant at 2.2 °C and 34.8, respectively.

3.2. Biological parameters

Mesozooplankton biomass in the upper 150 m (epipelagic zone) was slightly higher (WAST: 11.39–3.32 mg C m⁻³, CAST: 9.83–1.84 mg C m⁻³) than bacterial biomass (WAST: 3.31–0.93 mg C m⁻³, CAST: 2.00–1.32 mg C m⁻³) at both stations (Fig. 2). In the upper part of the OMZ (200–400 m), below the thermo- and halocline, the biomass profiles of the two biota were different: the mesozooplankton biomass was sharply reduced to a minimum of 0.26 mg C m⁻³ at WAST and 0.08 mg C m⁻³ at CAST, while the bacterial biomass was increased. At CAST, a pronounced bacterial maximum of 12.42 mg C m⁻³ occurred in the upper part of the OMZ where the oxygen concentrations fell abruptly just beneath the discontinuity layer. The bacterial biomass at WAST showed a smaller peak of 0.75 mg C m⁻³ in this zone. Below the upper part of the OMZ, the mesozooplankton biomass decreased almost steadily to 0.02 mg C m⁻³ at 50 m above bottom (mab), whereas the bacterial biomass was more or less stable, varying between 1.18–1.56 mg C m⁻³ at WAST and 0.53–1.13 mg C m⁻³ at CAST below 700 m. As a result, the biomass ratio of bacteria to mesozooplankton increased with increasing depth.

4. Discussion

Information about concomitantly taken samples of bacteria and zooplankton is sparse for the deep-sea (see also Yamaguchi et al., 2002) and, hence, the knowledge about the importance of these biotic groups in the deep-sea ecosystem is limited. This research note contributes to the knowledge about the distribution and ecological role of these groups in the deep ocean's interior. We will outline possible interactions of zooplankton and bacteria with particulate and dissolved organic material expressed as carbon concentrations. We are aware

that our data set is sparse, which makes the results somewhat arguable, however, we will show that our values are in the same range than other published data.

4.1. Epipelagic zone

For some stations close to our sites, Garrison et al. (2000) stated that the abundance of larger sized phytoplankton such as diatoms was increased during the late NE monsoon and the late SW monsoon and that the zooplankton removed about 50% of the daily phytoplankton production. During the less productive early NE monsoon and the intermonsoons, on the other hand, carbon cycling by the microbial community predominated. Our investigation during the late NE monsoon showed that zooplankton biomass exceeded that of bacteria in the epipelagic zone at WAST and CAST. Therefore, we suppose that the system was primarily driven by a “traditional” food chain during the time of our sampling. Overall, Garrison et al. (2000) found little spatial variation for heterotrophic bacteria in the Arabian Sea. The abundance ranged between 1.9×10^{10} and 1.0×10^{12} cells m⁻³ in the upper 100 m of the water column. These values are similar to our values of 1.1 – 2.2×10^{11} cells m⁻³ in this layer.

4.2. Mesopelagic zone

Our results are in accord with those of Raghukumar et al. (2001). They found an increased bacterial abundance between 250 and 500 m in the OMZ of the eastern and central Arabian Sea. This could be due to an increase in nitrifying bacteria (both ammonium and nitrite oxidizers), which are of great importance in oxygen minimum zones as stated by Ward et al. (1989) for a site off Peru. Especially at CAST, the bacterial biomass exceeded the biomass of mesozooplankton in the upper part of the OMZ, where the oxygen minimum was most extensive and not disturbed by filaments of oxygenated water.

The vertical decrease in abundance of mesozooplankton (see Koppelman et al., 2003) was most accentuated for size classes larger than 0.5 mm compared to the smallest fraction (<0.5 mm).

Among the mesozooplankton, however, several taxa (*Pleuromamma* spp., *Metridia* spp., *Eucalanus* spp., *Rhincalanus nasutus*, *Lucicutia* spp., Augaptilidae, Heterorhabdidae and *Conea rapax*) showed elevated standing stocks in the OMZ during night (Fabian et al., 2005). Organisms living in this zone often have evolved special adaptations to survive low oxygen concentrations (see Childress and Seibel, 1998); this zone can act as a refuge from predation (e.g. Alldredge et al., 1984).

4.3. Bathypelagic zone

Below 600–800 m depth, the bacterial abundance and distribution patterns at WAST and CAST are similar to data published by Hansell and Ducklow (2003) for stations near our sites and during different seasons. Yamaguchi et al. (2002) stated that the contribution of bacterial biomass to total plankton biomass (bacteria, phytoplankton, proto- and metazooplankton) reached 80% between 3000 and 4000 m in the Pacific Ocean because the decrease of mesozooplankton biomass with depth was much stronger than that of bacterial biomass. These results are in accord with our study, where the bacterial carbon biomass made up to 99% of the total of bacterial and mesozooplankton biomass in the deepest sample at WAST (3550 m) and 94% at CAST (2500 m). Boetius et al. (2000) measured the bacterial abundance in the near bottom layer up to 1000 mab at several stations in the Arabian Sea concomitantly with our measurements in February 1998, and additionally in April 1997. Between 250 and 1000 mab, the reported counts (1×10^{10} cells m^{-3} as an average) were lower than our mean value of 1×10^{11} cells m^{-3} , although there was an increase with decreasing distance from the bottom, amounting to 5×10^{10} cells m^{-3} at 0.6–0.1 m above the bottom.

Our mesozooplankton data show a vertical pattern that parallels the profiles of sinking and suspended particulate organic carbon (POC) published for various ocean's (e.g. Loh and Bauer, 2000). Therefore, we assume that the zooplankton abundance in the deep-sea is coupled with the POC concentration, which, possibly, is more

extensively exploited by zooplankton in oligotrophic seas (see Koppelman et al., 2004). In the oceans interior, the distribution of free-living bacteria seems to be coupled with the distribution of dissolved organic carbon (DOC) (e.g. Hansell and Carlson, 1998; Loh and Bauer, 2000) and total organic carbon (TOC) (Hansell and Peltzer, 1998). Boetius et al. (2000) support this concept. They stated that, most likely, the pool of suspended particles and DOC is the main source of energy to the bacteria of the benthic nepheloid layer.

4.4. Vertical distribution of bacteria—worldwide comparison

We have compared the bacterial distributions in the deep Arabian Sea with data from other deep-water sites in the open ocean. The data were transcribed from published figures at different scales (Patterson et al., 1993; Dufour and Torr ton, 1996; Patching and Eardly, 1997; Nagata et al., 2000; Yamaguchi et al., 2002). We standardized the data to cells m^{-3} and plotted the distribution on a log-scale against depth (Fig. 3). Based on annual means of chlorophyll data provided by SeaWiFs for the years 1998–2003 at the sites examined in the studies mentioned above, the stations were arbitrary grouped into oligotrophic (<0.2 mg Chl a m^{-3}), mesotrophic (0.2–0.6 mg Chl a m^{-3}) and eutrophic (>0.6 mg Chl a m^{-3}) sites. Only bacteria data below 200 m are presented because the data points in the graphs were too close together in the upper water column for a differentiation. Below 600–800 m almost all values range between 1×10^{10} and 1×10^{11} cells m^{-3} ; an exception is the somewhat lower values (3×10^9 cells m^{-3}) in the deep water over the Cape Verde Plateau (NE Atlantic, south; Patching and Eardly, 1997). This data set and other data sets from oligotrophic regions exhibit the lowest values, whereas the highest values occurred at sites of higher primary productivity (see Fig. 3). Dufour and Torr ton (1996) also stated that bacterial abundance in deeper waters correlates with surface productivity. Hansell and Ducklow (2003) suggested that the bacterial abundance in the deep-sea reflects the long-term mean of the POC flux rather than episodic pulses. Solubilized

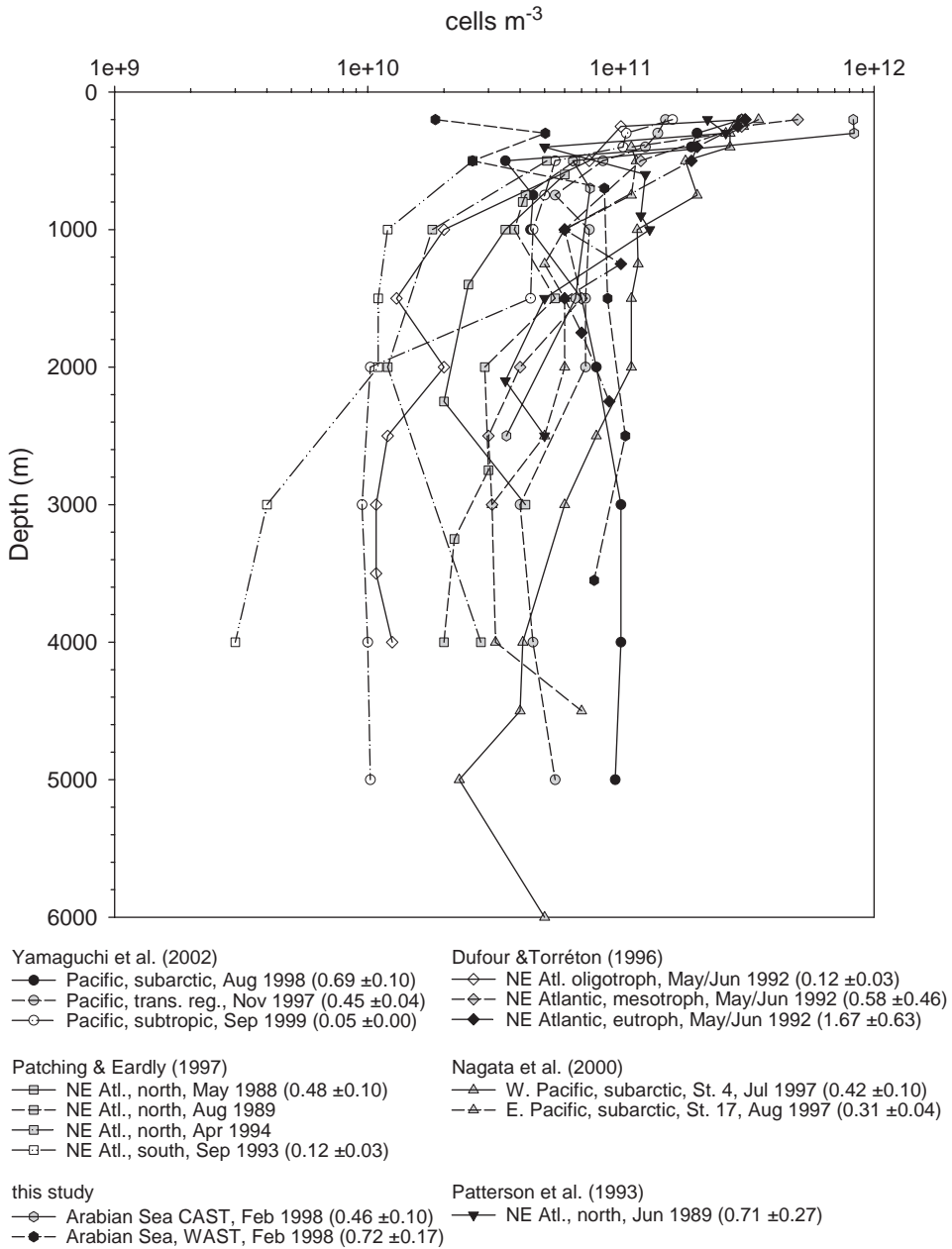


Fig. 3. Vertical distribution of bacterial concentration in different oceans below 200 m depth (compiled from different sources). open symbols = oligotrophic sites (<0.2 mg Chl a m⁻³), grey symbols = mesotrophic sites (0.2–0.6 mg Chl a m⁻³), black symbols = eutrophic sites (>0.6 mg Chl a m⁻³). Mean chlorophyll data (mg Chl a m⁻³) for the years 1998–2003 and standard deviations at the sites are given in parenthesis.

POC provides a continuous supply of oxidizable DOC in the deep-sea, however, in regionally different amounts. Since the POC flux is more or

less controlled by the surface production, the bacterial abundance reflects the annual primary production in the region. It is interesting that the

differentiation between productivity regimes becomes more clear in the deep mesopelagic zone and at bathypelagic depths and that an effect of the OMZ on the bathypelagic bacterial concentration (i.e. below the OMZ) is not visible in the Arabian Sea. Besides the fact that the bacterial abundances range within one order of magnitude irrespective of the ocean's basin, the most striking feature is that the decrease in abundance with increasing depth is small compared to the decrease of mesozooplankton, causing a high relative abundance of bacteria in the bathypelagic zone. Although, we do not know how many of the deep-sea bacteria are dormant, their potential for carbon remineralization seemed to be high in the deep-sea (see also Nagata et al. 2000).

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