

# 3. Role of Heterotrophic Bacteria in Marine Ecological Processes

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## Introduction

To the students of biology, the term bacterium elicits smallness, abundance, invidiousness, and completeness of single celled prokaryotes. Among other characteristics, ubiquity, nutritional versatility, infinite diversity and structural 'simplicity' come to one's mind. This smallest autonomous biotic entity in the living world is the most important functional unit. From the knowledge perceivable through the copious and burgeoning literature on these tiny creatures, it becomes a matter of great wonder that bacteria are so powerful and all-important in the functioning and stability of ecosystems. With less than 0.1 to 4  $\mu\text{m}$  in length, the abilities of decomposing innumerable organic molecules and several xenobiotics bring heterotrophic bacteria to the centre-stage of nutrient cycling within the earth's ecosystems.

All the world oceans are one contiguous water body covering over 70% of the earth's surface. With maximum depth exceeding 11000 meters, the 365 million square kilometers of the ocean area is the largest habitat. Stretching across from the Antarctic to North pole and, sprawling to surround most land masses, this aqueous continuum naturally experiences varied physical (salinity, temperature, light, density, turbidity, water-masses, upwelling, tides, currents, waves, climate-linked parameters, etc), chemical (concentrations of dissolved oxygen and other gasses, major constituents such as calcium, magnesium, fluoride, macro and micro-nutrients, dissolved organics, pollutants, etc) and biological (floral, faunal) characteristics. Other environmental parameters such as UV radiation,  $\text{H}_2\text{O}_2$ , superoxide and hydroxyl radicals (called reactive oxygen species) and ferric ion concentrations are known to exert significant influence on bacterial growth (Koga and Takumi, 1995; Gauthier, 2000; Ji-Dong Gu, Chapter 7). Most of these agents in aquatic environment can cause death and/or induce marine bacteria to enter viable-but-non-culturable state. Intriguingly enough, seawater is chemically the most complex fluid. With over 95 elements dissolved in it, depths up to 11022 m, pressure exceeding 1100 atmospheres, photosynthetically active radiation reaching less than 150 m, temperatures ranging from subzero to over

30°C, salinity varying from below 10 to over 40 PSU, the existence, processes and physiology of life in this milieu are great challenges.

In almost every possible niche, the fundamental property of bacteria is growth/ multiplication. As a result of growth and activity, heterotrophic bacteria in the marine sphere too are involved in a number of interrelated processes such as decomposition of complex molecules, respiration, mineralization, remineralization and, uptake of dissolved organic compounds and their conversion to particulate matter. Beginning the 1970s, there have been unprecedented discoveries related to marine microbial ecology. The realization that ubiquitous and self-regulating microbial communities provided the foundation to our understanding on the processes in marine food-web (Landry, 2001).

## Heterotrophy in the Marine Environment

Marine heterotrophy involving all animals and many microbes is a process by which autotrophically synthesised organic compounds are transformed and respired. In order to bring the importance of heterotrophic bacteria and their processes in the marine environment in to focus, an understanding on their abundance, distribution, production and, their involvement in nutrient cycling and how they are at the base of microbial food web is essential. Following phytoplankton blooms, the aggregation and sinking flux of organic matter (Takahashi, 1986; Bodungen et al., 1986) is an important aspect of material transport out of the euphotic zone. Heterotrophic bacteria utilize a large fraction of this sinking particulate organic matter (Wiebinga et al., 1997). Interaction between sinking organic matter (including fecal pellets and/or post-bloom aggregates) and heterotrophic bacteria - which often are the bulk of carbon biomass (Fuhrman et al., 1989; Cho and Azam, 1990; Ducklow, 2001) in pelagic ecosystems- is important in supporting life below euphotic zone. Thus, information on abundance and activity of heterotrophic bacteria is very useful to recognize their varied roles. Further, to appreciate the role of bacteria in the marine environment, one needs drawing the attention to three important marine

ecosystem processes. Bacterial utilization of labile fraction of dissolved organic matter (DOM), microbial loop and cycling of bio-essential elements. Despite their small size, heterotrophic bacteria are far more important in - and linked to - water column and sediment (benthic) processes. They degrade and eventually take up, grow on and respire an enormous variety of organic compounds. When bacteria decompose the organic compounds, they are oxidized, oxygen decreases and organic molecules ultimately disappear. In the marine environment, they are able to increase or decrease their activity over wider ranges of chemical and physical settings than any other group of organisms. Under favorable environmental conditions, they grow rapidly and, if conditions are unfavorable, they may become nearly dormant and wait until the favorable conditions return. Unlike these microbial communities, the higher organisms must continuously respire and must enter distinctive resting states.

We learn a great deal more on bacteria from their presence and abundance when we try to interpret energy flow. While above listed microbial processes appear overbearing and very profound, it is best to quote Kirchman and Williams (2000) from the seminal Book, *Microbial Ecology of the Oceans*. "We know about the many roles for heterotrophic bacteria in the oceans in addition to those outlined by Hobbie and Williams (1984)..... we do not even know what all the heterotrophic bacteria are doing in the oceans". This conundrum fittingly serves to recognize how much more is to be understood to decipher the various roles the varied bacteria found in the oceans.

There are innumerable recent and detailed investigations on heterotrophic bacterial abundance, activities and processes from Pacific, Atlantic, Antarctic and Indian oceans. The reader is referred to the recent Ocean Sciences Encyclopedia Series published by Academic Press in 2001 (Thorpe et al., 2001). While their abundance and role are realized substantially from the Pacific and Atlantic, the relatively scarce but important recent studies in one of the biologically unique regions, the Arabian Sea, have brought to light interesting newer information. Besides a general description of the roles and functions of heterotrophic bacteria, this chapter contains some recent advances made in our understanding of the role of heterotrophic prokaryotes in the Arabian Sea.

Both central and eastern regions of the Arabian Sea are biologically highly productive and changes in primary production are quite large on a seasonal basis (Banse, 1994; Madhupratap et al., 1996; Sarma et al., 2003). Physical forcing such as upwelling, winter cooling (Prasannakumar et al., 2001) and semi-annual reversal of monsoonal winds (Banse, 1994; Smith et

al., 1998) usher in such phenomenal dynamics in productivity. Regular oscillation in monsoonal atmospheric conditions drive near-surface currents affect mixed layer development and influence nutrient supply in this region experiencing relatively constant levels of illumination (Shetye et al., 1994; Smith et al., 1998). Thus, in the Arabian Sea, seasonal cycles in biological production greatly influence the biogeochemistry (Smith et al., 1998; Hansell and Peltzer, 1998; Burkill, 1999) and sedimentation rates (Nair et al., 1989; Haake et al., 1993). Further, just about two million square kilometer area in the Northern Arabian Sea is uniquely distinct with an extremely well developed oxygen minimum zone (OMZ, Swallow, 1984; Warren, 1994). This OMZ coincides with an extensive denitrification (Naqvi et al., 1994; 1998) at mid depths accounting for a third of the global marine denitrification (Naqvi, 2001).

## Bacterial Abundance and Distribution

The advent and application of epifluorescence microscopy to marine ecology in the 1970s ushered in an era of discoveries of previously unknown life-forms (Landry, 2001). We also made major advances in our understanding of trophic pathways and concepts involving the smallest organisms in the sea. There are estimates suggesting the bacterial abundance in the water column of the world oceans is  $10^{30}$  (Pomeroy et al., 1990). Often, these key players in ocean biology are the important components governing the biogeochemical processes in the oceans. Epifluorescence microscopic techniques, albeit labor intensive, have allowed direct counts to be made of microbes in seawater. The important findings are that bacteria are in large numbers and mostly small sized (0.2-0.4  $\mu\text{m}$  in diameter and 0.5 to 1.0  $\mu\text{m}$  in their largest dimension). While it was relatively easy to obtain numbers of bacteria, it had been difficult to agree upon an acceptable factor for converting numbers to biomass or carbon equivalents owing to diverse opinions of many research teams. Literature in the 1990s was burgeoning with a plethora of conversion factors ranging from 10 to 40fg C cell<sup>-1</sup> (Pomeroy and Joint, 1999) to figure out the carbon pool in marine bacteria. However, the consensus arrived by many recent investigations suggest an average of 11 fg C cell<sup>-1</sup> (Landry et al 2001). In comparison with data from other open-ocean observations (e.g., Ducklow et al., 1992; Kirchman et al., 1995), the heterotrophic bacterial stocks observed in the Arabian Sea are quite substantial (Table 1). High levels of primary production, excessive concentrations of DOC (Hansell and Peltzer, 1998), intense grazing

on picoplankton (Brown et al., 1999) and consequent supply of high dissolved organic matter facilitate their growth and abundance.

## Heterotrophic bacterial production

Ducklow (2000) defines bacterial production as *secondary production* in which bacterial biomass is synthesized primarily from organic precursors with some inorganic nutrients. A new era in the study of bacterial dynamics in the aquatic ecosystems was ushered in by the introduction of <sup>3</sup>H-thymidine (TdR) incorporation as a measurement of heterotrophic bacterial production for the first time by Fuhrman and Azam (1980) and some modifications to this method by Azam associates (Fuhrman et al 1980, Fuhrman and Azam, 1982). Despite some drawbacks (Winn and Karl, 1984; Robarts et al., 1993), it is the most widely used method for estimating bacterial production (Kemp et al., 1993). The bacterial production ranges from as low as 5.5 to as high as 285 mg C m<sup>-2</sup> d<sup>-1</sup> in the euphotic zones of the world oceans (Table 1). On an average, bacterial production in the open ocean Arabian Sea is about a quarter of the phytoplankton production and it exceeds primary production during the intermonsoon periods (Ramaiah et al., 1996).

Higher rates of bacterial production during low chlorophyll productivity have very important consequences in microbial loop (Madhupratap et al., 1996).

## Heterotrophic bacterial uptake of DOM

DOM is a complex mixture of carbon and nutrients and ocean is the largest pool of DOM. All organisms, including phytoplankton, macrophytes, zooplankton, fish, shell-fish, benthos and mammals in the ocean liberate DOM through a variety of physiological processes. Additional DOM is released when zooplankton fecal pellets and other forms of organic detritus decay. Heterotrophic bacteria are efficient in direct uptake of low-molecular weight (< ~500 Daltons) DOM. In addition, upon attaching, adsorbing or 'packaging' to labile particulates in the seawater, bacteria elaborate ectoenzymes, dissolve the easily assimilable fraction and convert such particulate organic carbon into their cell carbon component (Chrost, 1990; Azam et al 1993; Smith *et al*/1995). If not 'absorbed' as quickly upon its release by these microbes, due to chemical reactions, the DOM would

Table 1 Bacterioplankton Biomass and production in a few selected regions of the world Oceans (data from Ducklow, 2000, Ramaiah et al., 1996 and 2000 for Eastern Arabian Sea and Ramaiah et al unpublished for Bay of Bengal)

	<b>Euphotic zone (m)</b>	<b>Bacterial Biomass (mg C m<sup>-2</sup>)</b>	<b>Production (mg C m<sup>-2</sup>d<sup>-1</sup>)</b>	<b>Growth rates</b>
Arabian Sea	74	1148	257	0.18
N. Atlantic	50	1000	275	0.30
Equatorial				
Pacific, spring	120	1467	176	0.12
Sub North Pacific	80	1142	257	0.18
Ross Sea	45	217	5.5	0.25
Central Arabian Sea				
Intermonsoon	80	637	585	0.33
SuM	65	243	76	0.22
Eastern Arabian Sea				
SpIM	85	613	1371	0.44
SuM	60	443	314	0.21
Central Bay of Bengal				
SuM	45	1057	217	0.20
FIM	55	227	106	0.47
SpIM	65	104	59	0.57
Western Bay of Bengal				
SuM	35	673	155	0.23
FIM	45	662	635	0.12
SpIM	60	95	73	0.77

SuM: Summer Monsoon (Jun-Sept), SpIM: Spring Intermonsoon (Mar-May);

FIM: Fall Intermonsoon (Oct-Dec)

pool up the refractory portion and genuinely lost from the trophodynamic arena. Azam et al (1994) suggest that bacteria utilize DOM with highly variable carbon assimilation efficiency of 10-70%. Being the principal biotic components capable of assimilating DOM, heterotrophic bacteria, usually with large surface to volume ratios, are important in marine food webs and biogeochemical cycles (Ducklow et al., 2001).

Although several intricate physical and chemical processes influence the biological activities throughout the water column, below the euphotic zone, the *secondary production* in terms of heterotrophic bacterial growth is paramount in extending the life in to the deep ocean. Below euphotic zone too, heterotrophic bacteria grow and reproduce by assimilating dissolved organic matter and, by dissolving and reprocessing most portions of the particulates raining down from the upper columns. The microzooplankton (ciliates, heterotrophic nanoflagellates, protists, etc) and many other macrofaunal components in the deep waters and in the benthic realms must be deriving a greater portion of their nutrition through the explicit uptake of dissolved organic matter by bacteria and, consumption of bacteria by bacterivores (Strom, 2000). By recovering the released DOM, which would otherwise accumulate and can turn refractory, bacteria initiate the microbial loop.

## Heterotrophic bacteria and Microbial loop

The new concept in marine ecology that came to being in the 1980s is the microbial loop proposed by Farooq Azam and coworkers (Azam et al., 1983). Microbial loop can be described as a complicated network of biota and processes based on the flow of detritus-based energy through the food web. In microbial loop, heterotrophic bacteria, analogous to photosynthetic autotrophs, are at the base (Fig 1). This understanding has done violence to our earlier understanding on the marine food chain. In that, prior to the realization by Jannasch and Jones (1959) that bacteria were numerous in the oceans, the autecologists who could grow only a few types of bacteria led some to think that prokaryotes were not central parts of biological processes in the ocean. Bacteria, at best, were believed only as decomposers of organic materials and producers of inorganic nutrients to support phytoplankton growth (Kirchman and Williams, 2000). Heterotrophic bacteria form food for protozoa, invertebrate larvae and many large zooplankton and, regenerate dissolved nutrients required for marine photosynthesis and formation of newer organic biomass (Fig 2). By a critical evaluation of the information on various biological parameters analyzed

during the Joint Global Ocean Flux Study in the eastern Arabian Sea, Madhupratap et al (1996) and Mangesh (2000) provided a reasonable explanation to the "Arabian Sea mixed-layer mesozooplankton stable biomass paradox". Despite the very meager photosynthetic production during the inter-monsoon months of October-December and April-June, the biomass of mesozooplankton (animals in 200-500  $\mu\text{m}$  size range) in mixed-layer depths remains almost invariant. Recognition of albeit of long, energy-inefficient microbial loop with heterotrophic bacteria at the base and microzooplankton linking bacteria to mesozooplankton is an important finding that highlighted the significance of microbial loop in the upper layer biological processes of the Arabian Sea.

In spite of the new methods and instruments, the problem of how to measure the various aspects of marine heterotrophy has not been easy to resolve. Paradoxically enough, the continuous processes that remove bacteria (death and grazing) occur at the same time as production (Landry 2001). Thus, neither a steady state nor changes in the numbers of bacteria necessarily reflect bacterial production or, lack of it. Despite our progress in measuring rates and identifying the role of bacteria in the heterotrophic and other processes, we are uncertain about the species composition of the community. When we come to know of the identity of all the bacteria in the sea, as Rappe and Giovannoni (2000) ponder, we could then be able to answer the question whether the sea is populated with microbial specialists or generalists.

## Heterotrophic bacteria and Nutrient Cycles

In any ecosystem, the energy flow is in one direction but the nutrients are often recycled repeatedly (Campbell, 1983). Nitrogenous, carbonaceous, phosphatic, silicate nutrients as well as many other bio-essential elements viz., O, H, S, Fe, K, Ca, Mn, Co, Cu, Zn, Se, among a few others, are appropriately processed, transformed and incorporated into organic constituents of all life-forms. Maintenance of life thus depends on continued recycling of inorganic materials and decomposition of organic matter to produce substrates required for all types of life-functions. This *movement* of many substances while creating energy can be termed the biogeochemical cycle (Fig 3). In principle, this cycling of materials can be described in terms of the pools of concerned substances in soluble, organically bound or gaseous forms. One of the major interests of the contemporary biogeochemists is to quantify the concerned substance/nutrient in any pool or, all possible pools, so that the flow rates between the pools can be realized in order to understand the nutrient recycling

mechanisms. This interest is not only to detect the abnormalities due largely to anthropogenic perturbations, and to realize what it takes at the global ecosystem level to correct the flow rates but also to check if the system can return to equilibrium, somehow. We do not as yet know enough about normal pool sizes and turnover times of the biogeochemical cycles. Human activities leading to habitat destruction/alteration or dumping large

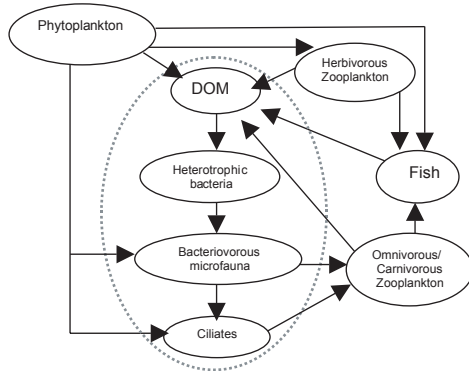


Figure 1. A generalized concept of microbial-loop. Dissolved organic matter (DOM) pool is almost exclusively assimilated by bacteria that are instrumental in sustaining herbivorous microfauna and running the microbial loop (inside the dotted area) and energy flow to zooplankton and fish.

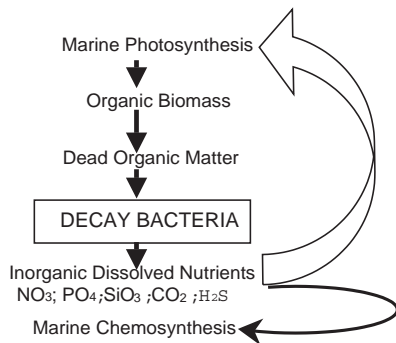


Figure 2. Central role of decay (heterotrophic) bacteria in formation of inorganic dissolved nutrients and making them available for photosynthesis, which is the basic and one of the major drivers of marine ecological processes. While large arrows are to indicate flow of regenerated inorganic nutrients both for autotrophic phytoplankton and chemolithotrophic organisms, smaller ones are to show the linkages to different processes.

amounts of materials are affecting the global ecosystems and certainly bringing about undesired ecological imbalances.

Bacteria are the principal agents that are variously involved in the global biogeochemical cycles. As a community, they have assemblages which adjust and make home of any situation. In that, many of them are undemanding (not-so-specific) in their nutrient

requirements, have wide tolerance of environmental conditions thus continue to grow and reproduce on a variety of substrates under a variety of conditions ushering in situations of non-competition. They usually grow rapidly and occupy any microhabitat yet retain the potential to achieve dormancy whenever, wherever and however needed. Many of them not only produce toxins (antibiotics) but can tolerate/overcome ill effects of toxins from other organisms. In addition, the heterotrophic bacteria ( $\equiv$ decay bacteria) are pivotal in remineralizing the dead organic matter releasing many inorganic dissolved nutrients such as  $\text{NO}_3$ ,  $\text{PO}_4$ ,  $\text{SiO}_3$ ,  $\text{CO}_2$ ,  $\text{H}_2\text{S}$  etc which govern the marine chemosynthesis and fuel the biogeochemistry of the oceans.

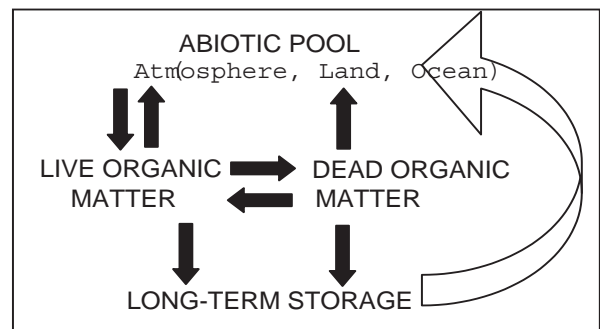


Figure 3: A generalized biogeochemical cycling of biologically essential elements between biotic and abiotic pools. Microorganisms play an important role in mobilizing elements between these pools including the ones in the long-term storage.

## Carbon cycle

Carbon has a unique position as the component of life, energy flow and even climate regulation (Carlson et al., 2000). Complex, stable carbon compounds such as proteins, carbohydrates, nucleic acids are the fundamental building blocks of life. Carbon is cycled through all of the earth's major reservoirs: lithosphere, hydrosphere, atmosphere, and, biosphere albeit at different rates (Brock et. al., 1994). The involvement of microbes, in particular heterotrophic bacteria in the turnover of carbon, lies in their capacity of decomposition. For example, the photosynthetically formed high energy organic carbon compounds, universally represented by  $\text{CH}_2\text{O}$ , are degraded or oxidized by bacteria and other chemoorganotrophs (fermentors, anaerobes, aerobes) resulting in either methane by methanogens or, carbon dioxide by chemoorganotrophs. Eventually, methane is oxidized to  $\text{CO}_2$  by methanotrophs. Hence, all carbon returns finally to  $\text{CO}_2$  from which autotrophic metabolism once again begins the cycle (Fig 4). Carbon is absorbed by the ocean in its dissolved gaseous  $\text{CO}_2$  form and, the algae (phytoplankton) incorporate it through photosynthesis in the surface waters where light is

available. On a global basis, marine phytoplankters in the euphotic zone of 50-150m of the upper water column are responsible for more than a third of the gross photosynthetic production of  $50 \times 10^9$  tons  $C y^{-1}$ . With an estimated bacterial abundance of ca  $10^{30}$  cells, and  $11 \text{ fg } C \text{ cell}^{-1}$ , bacteria account for ca  $1.1 \times 10^9$  tons which is more than a third of the  $3 \times 10^9$  tons standing stock of total marine biotic carbon (Carlson et al., 2000). As they are known for tolerating and growing in a wide variety of environmental conditions, the marine heterotrophic bacteria are extremely important in the cycling of carbon between atmosphere and the ocean. Most portions of the photosynthetically formed carbon compounds including the particulate, detrital and dissolved organic carbon are utilized by heterotrophs as energy sources and remineralized to  $CO_2$  via respiration. In order that the other nutrients such as nitrates, silicates, phosphates, are not lost out of the euphotic zone, the rate of remineralization has to be very rapid and, heterotrophic bacteria are very efficient remineralizers (Chandramohan and Ramaiah, 1987, Sarma et al, 2003).

and gas to drive the world's economy. The burning of fossil fuel releases large quantities of  $CO_2$  into the atmosphere, which may accumulate over time or can be incorporated into plant material or be absorbed back into the sea.

As Kirchman and Williams (2000) suggest, carbon is the currency of choice for examining the fate of primary production in the oceans; in assessing climate change; for addressing questions concerning carbon cycle and for quantifying the standing stocks and production rates of various microbial communities in the marine ecosystems. Quantification of the flux of DOM through bacteria to higher trophic levels, and the contribution of heterotrophic bacteria to mineralization of carbon and nitrogen are important requirements for an overall perspective of seeking an understanding of the role of microbes in food web dynamics and biogeochemical cycles in the oceans. Much scientific effort supported by International Geo-sphere Biosphere Program is ongoing for finding out how much  $CO_2$  held in the deep waters is going to be available to be absorbed by the land. Global warming might warm the oceans, change the circulation of minerals in the water and reduce the amount of phytoplankton. Will that mean more carbon dioxide remaining in the atmosphere?

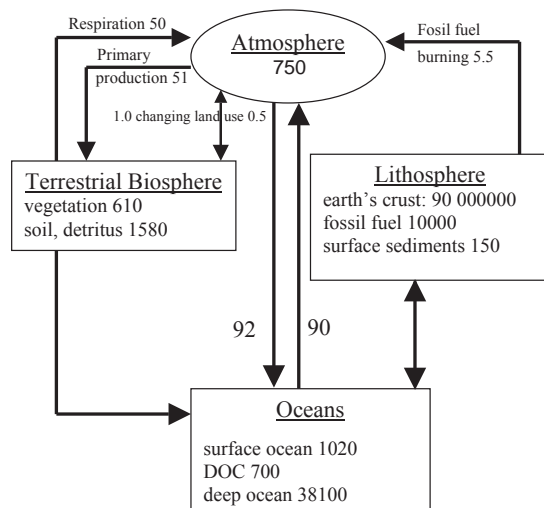


Figure 4 Global carbon cycle with reservoirs of the atmosphere, lithosphere, terrestrial biosphere and oceans. All stocks of carbon and exchanges expressed as  $10^9$  tonnes. Data adapted from Carlson et al. (2001)

Organic carbon is passed through the food web. In that, phytoplankton, bacteria and other small organisms are consumed by herbivores, omnivores or, even by predators. Yet, a significant percentage of the carbon is discarded in the remains of organisms which sinks to the seafloor to be buried in the sediments and, if subjected to the proper combination of pressure and temperature, will transform into hydrocarbons. These hydrocarbons are then developed into the fossil fuels and extracted as oil

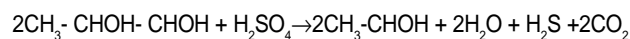
## Sulphur Cycle

As sulphur is present in a number of vitamins (thiamine, biotin, lipoic acid) and has structural role in amino acids cysteine and methionine, it is absolutely required by organisms. Sulphur, also with a number of oxidation states, undergoes a number of chemical transformations in nature carried out exclusively by microorganisms (Brock et al., 1994). The three very significant oxidation states are sulfhydryl (-2:  $R-SH$ ,  $HS^-$ ), elemental sulphur ( $S^0$ ) and sulphate ( $SO_4^{2+}$ ). While the bulk of it is in rocks and sediments, oceans serve as the most significant reservoir of sulphur for the biosphere activities.

Anthropogenic activities in the last 100 or so years have disturbed the natural sulphur cycle, rather drastically. The burning of fossil fuels burdens the air with excessive sulphur dioxide, which is washed out by rain into the soil and aquatic environments. Industrialization adds considerable amounts of sulphur dioxide and hydrogen sulphide to the atmosphere. Decomposition of proteins by many kinds of bacteria may release sulphate under aerobic condition or hydrogen sulphide under anaerobic condition. Volatile sulphur compounds such as dimethyl sulphide (DMS), produced primarily in the marine environment, are also produced under anaerobic decay. These DMS molecules, some 45 million tons annually, when oxidized to sulphate

species, are believed to be of great significance as nuclei for cloud formation (Kumar et al., 2002). The DMS undergoes photochemical oxidation to methane sulphonic acid, sulphur dioxide and sulphate (Brock et al., 1994).

As mentioned previously, microbes are not only responsible for oxidation of organic substances but also for reduction of certain inorganic compounds (Lokabharathi et al 2001). For example, under anoxic conditions the principal source of sulphide is sulphate reduction by anaerobic bacteria such as sulphate reducing bacteria (e.g., *Desulfovibrio*). Thus, with highly reduced organic substrates (e.g., lactic acid) as carbon sources and sulphate as electron acceptor, the oxidation by SRB is as follows:



The sulphide, thiosulphate and sulphur ( $\text{S}^{2-}$ ) are used up by microorganisms such as *Thiobacillus denitrificans* (Lokabharathi et al., 2001). Also, the  $\text{H}_2\text{S}$  produced by anaerobic decay may precipitate metals as sulphides rendering black coloration to sediments. While chemosynthetic (e.g., *Thiobacillus*, *Beggiatoa*, *Thiothrix*) bacteria oxidize sulphides under aerobic conditions, the photosynthetic bacteria (*Chlorobium*, *Chromatium*) oxidize them under anaerobic conditions.

Sulphate is one of the most common anions in water and is present in especially large amounts in the seawater. Most microorganisms and plants can use sulfate as their sole source converting it to sulphydryl compounds by a process known as assimilatory sulphate reduction. Under anaerobic conditions, most microbes by dissimilatory sulphate reduction (sulphate serves as an electron acceptor) produce  $\text{H}_2\text{S}$  which is toxic to many life forms and precipitates metals as sulphides. In any case, sulphate reduction is the most important means of  $\text{H}_2\text{S}$  formation in the sea. This  $\text{H}_2\text{S}$  is an exclusive requirement for the anaerobic photosynthetic bacteria. Although many heterotrophic bacteria including actinomycetes can oxidize  $\text{H}_2\text{S}$ , the chemosynthetic bacteria are far more important. Lokabharathi (Chapter 4) and Kerkar (Chapter 5) have dealt on organisms involved sulphur cycle in greater details.

## Phosphorus Cycle

Phosphorus occurs in organic and inorganic forms in nature. Its use by living organisms is primarily in nucleic acids, phospholipids and ATP. When it comes to meeting their phosphorus requirement, which is also a macronutrient like carbon, nitrogen and sulphur, the most important thing the heterotrophic bacteria do is that they directly take up inorganic phosphate and

grow (Pomeroy et al., 1984). The organic moieties of phosphorus are utilized by living organisms after they hydrolyze the organic phosphate ester by phosphatases to release the inorganic phosphate and incorporate it for cellular functions. Oceans are one of phosphorus's main reserves albeit it is in much lower concentrations. Further, its burial below the euphotic zone means much lesser availability for photosynthetic activities. As implied by Pomeroy et al (1984), the ability of direct up take of inorganic phosphate by bacteria is very important as flagellates, ciliates and other

microfauna can meet their phosphorus requirement through bacterivory instead of elaborating phosphatases into the surrounding environment. Due to higher primary productivity in the upwelling regions and rapid transit of organic and biogenic material through the water column, the accumulation of phosphorus in the form of phosphorite ( $\text{CaPO}_4$ ) is substantial along continental margins (Rao et al., 2001). Phosphorite is not an easy source of phosphate for microbial/general biological activities. Strong acid producing groups of bacteria including the anaerobes play a crucial role in solubilizing this mineral. Indirectly, some bacteria solubilize the bound phosphate by producing acidic end products. Aside these biological activities, the physical (upwelling, lateral advection), geological (tectonic, sedimentological) and chemical (pH, availability of iron, calcium or certain organic ligands) processes are also vital in the turnover of this element.

The quantitative abundance of different bacterial groups involved in producing certain enzymes required for catabolizing different substances is listed in Table 2 for an assessment of the potential of heterotrophic bacteria in bio-essential elemental cycling. Heterotrophic bacterial decay of organic matter also releases iron, manganese, cobalt and other micronutrients necessary for plant growth. Thus, cycling of all the bio-essential elements is intricately linked to the heterotrophic bacterial processes in the environment. In addition to supporting life throughout the water column, bacteria are relevant in the benthic food chain as well. Ansari (Chapter 18) has dealt with this aspect to give the perspective of bacteria governed benthic-trophodynamics. The hydrothermal vent biology is almost entirely driven by chemolithotrophic bacteria symbiotically harbored by many macrofauna inhabiting the seafloor spreading zones (Jannasch, 1990, Brock et al., 1994).

## Nitrogen Cycle

Microorganisms, fungi and bacteria in particular are of great importance in the nitrogen cycling in nature (Brock et al., 1994). Nitrogen is a key constituent of

proteins and nucleic acids. It forms a number of compounds with oxidation states of R-NH<sub>2</sub> (organic N), NH<sub>3</sub>, N<sub>2</sub>, N<sub>2</sub>O, NO, NO<sub>2</sub><sup>-</sup>, NO<sub>2</sub> and NO<sub>3</sub><sup>-</sup> increasing from -3 (as in R-NH<sub>2</sub>) to +5 (in NO<sub>3</sub><sup>-</sup>). In terms of energy yield, nitrate (i.e., the redox pair: glucose +NO<sub>3</sub> yielding 649 kcal/mol) acts nearly equivalent to oxygen (glucose +O<sub>2</sub> yielding 686 kcal/mol) as a terminal electron acceptor when reduced all the way to dinitrogen gas via denitrification (Sherr and Sherr 2000). Bacteria are responsible for both decomposition of proteins, peptides, chitin, urea, amino acids, nucleic acids among many others and, chemical conversions between the various oxidation states of nitrogen including ammonium, nitrogen gas, nitrite and nitrate. For example, chitin, a complex marine polymer, is broken down by bacteria which produce an array of enzymes leading to formation of glucose and CO<sub>2</sub>. Also, the rate of glucose formation (and utilization) by chitinoclastic bacteria is quite impressive (Fig 5).

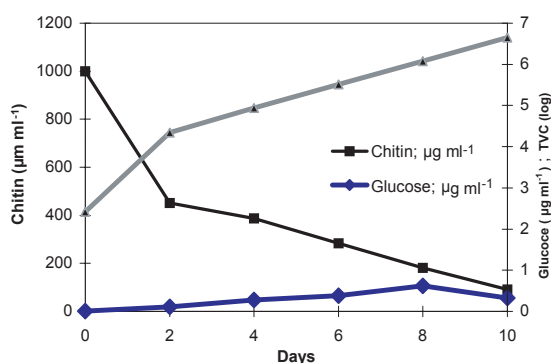


Figure 5: Utilization of chitin by an isolate of *Vibrio harveyi* (BC7) and subsequent levels of sugars in terms of glucose and growth in terms of total viable counts during a 10-day experiment (Data from Ramaiah, 1989)

One must remember that owing to quite high C/N ratios in most plant matter, the nitrogen is always in short supply during decomposition. Thus, the given amount of organic nitrogen is repeatedly recycled through decomposer microbes and most of the nitrogen used by plants comes from mineralization of existing organic material. The main processes involved in the global nitrogen cycle (Fig 6) are:

- *Nitrification* in which ammonium is oxidized to nitrite and nitrate
- *Nitrate reduction* is a process leading to nitrite and ammonium formation
- *Denitrification* usually leading to reduction of nitrite to gaseous nitrogen
- *Nitrogen fixation* leading to reduction of dinitrogen gas to ammonium.

In the marine nitrogen cycling, conversions among inorganic and organic species are generally biologically mediated (Capone 2000). The principal transformations of the marine N cycle include:

- Uptake and incorporation of inorganic forms of nitrogen into organic forms
- Regeneration and release of inorganic form (primarily as NH<sub>4</sub>) from organic forms
- Oxidation of ammonium and nitrite in nitrification.
- Reduction of NO<sub>3</sub> or NO<sub>2</sub> to gaseous forms, N<sub>2</sub> and N<sub>2</sub>O in denitrification and,
- Reduction of N<sub>2</sub> to NH<sub>4</sub>.

Nitrogen availability in the marine euphotic zone is critical for primary productivity and export production and, therefore, of carbon dynamics in the diverse and expansive oceanic habitats. Many physical processes and biological reactions of nitrogen contribute to its availability and the relative fertility of the upper ocean (Capone 2000). The marine nitrogen cycle is intimately connected to the atmosphere. As mentioned above, several gaseous species of nitrogen (i.e., N<sub>2</sub>, N<sub>2</sub>O, NO, NH<sub>3</sub>) can exchange readily with atmospheric pools. Many of the combined forms of nitrogen (i.e., NO<sub>3</sub>, NH<sub>4</sub><sup>+</sup>, DON) can enter the sea through atmospheric deposition. While carbon, may never be in limiting concentrations for photosynthesis, critical trace nutrients such as Fe, required for many of the reactions of the nitrogen cycle, have an important atmospheric path to the sea through deposition of Fe-rich aeolian dust (Capone, 2000). Fe additions have been shown to promote NO<sub>3</sub> draw-down in some high nutrient low chlorophyll (HNLC) areas such as the equatorial Pacific (Martin et al., 1994; Paerl et al., 1994; Paerl and Zehr, 2000).

Bacteria are dominant in most of these transformations. Many aerobic bacteria are facultative nitrate respirers and substitute NO<sub>3</sub> as terminal electron acceptor when oxygen is absent or extremely minimum as is the case in OMZ in the Arabian Sea (Naqvi, 1994). In the OMZ depths from ca 150 to 1200 m, there is intense denitrification reducing NO<sub>3</sub> through sequential steps to nitrogen gas (NO<sub>3</sub> → NO<sub>2</sub> → NO → N<sub>2</sub>O → N<sub>2</sub>). A large percent of heterotrophic bacteria have been found to elaborate nitrate reductase in the depth zone of 150-1000m implying the presence of bacterial communities unique to denitrification zone (Table 2). Further as far higher fractions of culturable bacteria were capable of growth on 1/5 strength nutrient agar, it is suggested that the open ocean heterotrophic bacteria in the Arabian Sea have adapted to oligotrophy and a large percentages of them elaborate a variety of degradative enzymes



(Table 2). In the Arabian Sea, the estimated carbon demands for denitrification in the 200-1000 m column range from ca. 155 mg C m<sup>-2</sup> d<sup>-1</sup> (Naqvi et al., 1996), 519 - 2274 mg C m<sup>-2</sup> d<sup>-1</sup> (calculated from Ducklow, 1993) to 346-518 mg C m<sup>-2</sup> d<sup>-1</sup> (derived from Banse 1994). These carbon demands are apparently met through export fluxes (Honjo et al., 1999), lateral advection (Naqvi et al., 1996) or by particulates (Kumar et al., 1998, Ramaiah et al., 2000). It is, however, important to note that denitrification by heterotrophic bacteria in the intermediate depths of the Arabian Sea is phenomenal accounting for over a third of the global oceanic denitrification (Naqvi et al., 1982, 1996, 2000).

Nitrous oxide, a product of both marine nitrification and denitrification is a potent greenhouse gas (Naqvi, 2001). Through marine nitrogen cycle, atmospheric nitrogen deposition is expected to increase with future population growth and development in coastal areas. Anticipated changes in terrestrial physiography through shifts in climate and land-use patterns will affect nitrogen and, thereby, carbon cycles in the marine arena (Capone, 2000). Meso-scale manipulative experiments examining biological and

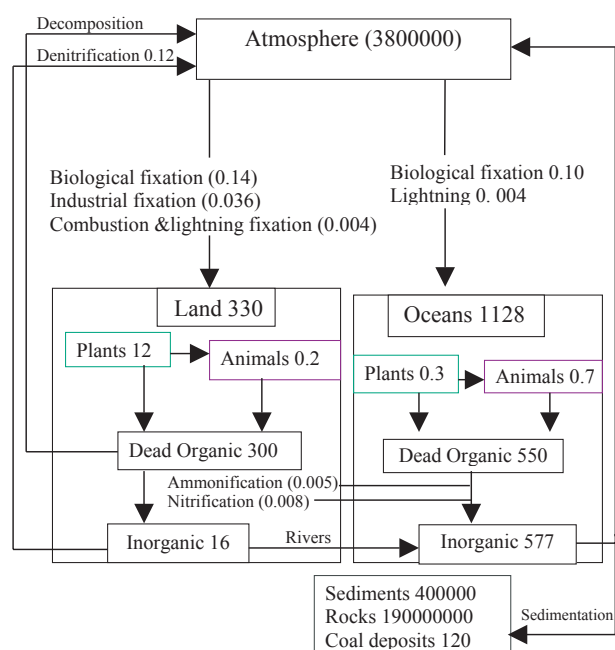


Figure 6. Global nitrogen cycle with major fluxes between atmosphere, lithosphere and oceans. Available flux rates indicated in figures (usually in decimals x 10<sup>9</sup> tonnes per year). Data from Brock et al (1994).

Table 2. Mean colony forming units (CFU) of bacteria (no L<sup>-1</sup>) on one-strength nutrient agar (1S NA) and their comparative percent on 0.5, 0.2 and 0.1 strengths of NA. Data pooled from five different sampling locations along 64 °E in the Arabian Sea. Elaboration of different degradative enzymes by heterotrophic bacteria isolated from different depths. Asterisk denotes number of isolates from different depths tested for various enzymes. Data from Ramaiah unpublished observations

Depth (m)	comparative % of CFU on different strengths of NA				No of isolates*	% of isolates +ve for different enzymes			
	1 S NA	0.5S	0.2S	0.1S		Amylase	Lipase	Protease	NO3 Reductase
1	9466	108	172	142	337	32	23	70	33
10	8967	119	138	139	286	28	20	61	36
20	7943	126	152	152	236	31	34	62	40
40	5676	139	202	143	365	36	42	72	44
60	4943	104	188	155	294	46	35	77	52
80	4100	115	190	162	258	29	50	71	51
100	3963	135	187	119	305	58	51	85	47
120	3469	126	196	202	266	42	52	55	52
150	2969	137	179	163	263	56	48	72	55
200	1711	169	202	174	198	19	37	73	42
300	1511	187	250	143	223	23	60	58	42
400	1196	165	214	169	312	27	24	51	56
500	907	206	222	129	243	29	29	57	60
750	1303	211	195	119	169	32	40	76	62
1000	723	196	232	139	184	37	42	73	65
1200	518	218	203	126	192	31	33	78	68
1500	312	176	194	149	237	48	30	66	43
1750	331	189	233	148	214	40	34	76	33
2000	211	202	219	163	144	42	38	71	38

chemical responses and air-sea gas exchanges in response to perturbations such as ocean Fe fertilization should clearly consider nitrogen dynamics.

## Heterotrophic bacteria and Marine Pollution Bioremediation

The very basic functional characteristic of decomposition by heterotrophic bacteria is of considerable ecological and economic importance in pollution clean-up. Native heterotrophic microflora capable of degrading a variety of environmental and human health-hazardous toxic substances are quite common in the marine environment. The ability of such heterotrophic prokaryotes to transform many highly toxic wastes to substances that are nontoxic, bioavailable and utilizable by other forms of life is very important in ecosystem stability. A variety of pollutants such as petroleum hydrocarbons, xenobiotics, synthetic plastics, heavy metals and untreated sewage out-fall can be problematic to coastal environments. Accidental spills of crude oils, perpetual leakage and bilge washings from marine crafts add large amounts of petroleum hydrocarbon moieties. Modern man manufactures and uses innumerable xenobiotic substances such as pesticides, insecticides, fungicides apart from plastics. Industrial, automobile, agricultural and animal husbandry practices make use of a variety of organic (fertilizers) and inorganic (heavy metal, non-metal) substances. These practices generate large quantities of wastes, some of which highly toxic, and they find ways into aquatic environment through land runoffs, ground water and /or direct dumping. Petroleum hydrocarbons, many xenobiotics and domestic sewage are carbon sources for certain microbial groups and can be attacked by these specialists.

Although some toxic xenobiotics have been recalcitrant to microbial attack, a large number of them have been degraded under suitable environmental conditions by native microflora. Microorganisms capable of resistance and, detoxification of many xenobiotics -and some heavy metals- are reported to possess plasmids conferring certain extraordinary properties to bacteria. There have been innumerable recent studies examining marine bacteria for pollution bioremediation and in many other biotechnological applications. The reader is referred to Brock et al (1994); Zilinskas et al (1995), Colwell (2000) and Singleton et al (2000) for an appreciation of the innumerable 'newer' jobs heterotrophic bacteria are capable of undertaking.

The microbially mediated processes such as DOM assimilation, microbial loop, nutrient regeneration, pollution clearance and, the overall ecosystem stability

- and interactions (i.e., symbiotic, parasitic/pathogenic, commensalistic) are fundamental and integral events of the marine environment. Apart of from these processes essential for ecosystem functioning and stability, a few groups of heterotrophic bacteria are involved in causing diseases in marine plants and animals (Kinne, 1980). The economic losses due to diseases in the marine environment both in feral and cultivated populations are of paramount importance. Karunasagar (Chapter 13) has listed numerous pathogenic organisms of concern in aquaculture. In this contiguous milieu that is "liquid planet", the spread of both invasive (can compete with the native flora in an alien location) and pathogenic bacteria is of greater concern for ecosystem up keep and for safe guarding native flora and fauna from economic devastation.

In conclusion, the roles heterotrophic bacteria play, are profound in the overall normal functioning, stability and continuance of the marine ecological processes. While the benefits due to these microbial communities are insurmountable, the objectionably malicious jobs, though a few in number, are also of ecological, economical and long term consequences. Their ecological dynamics, identity, roles in food web and biogeochemical cycles are being better understood with application of technology and precise measurements.

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## References

- Azam, F., Martinez, J., Smith, D. C., 1993. Bacteria-organic matter coupling on marine aggregates; In: Guerrero, R., Pedros-Alio, C (Eds), Trends in Microbial Ecology. Spanish Society for Microbiology, Barcelona, pp 410-414.
- Azam, F., Steward, G. F., Smith, D. C., Ducklow, H. W., 1994. Significance of bacterial in carbon fluxes in the Arabian Sea. Proceedings of the Indian Academy of Sciences (Earth and Planetary Science) 103, 341-351.
- Azam, F., Fenchel, T., Field, J. G., Gray, J.S., Meyer-Reil, L.A., and Thingstad, F., 1983. The ecological role of water column microbes in the sea. Marine Ecology Progress Series, 10, 257-263
- Banse, K., 1994. On the coupling of hydrography, phytoplankton, zooplankton offshore in the Arabian Sea and organic particles settling to depth. In: Lal, D (Ed), Biogeochemistry of the Arabian Sea, Indian Academy of Sciences, Bangalore, pp 125-161.
- Bodungen, B. van, Smetacek V., Tilzer M. M., Zeitzschel, B., 1986. Primary production and sedimentation during spring in the Antarctic Peninsula region. Deep Sea Research 33, 177-194.
- Brock, T. D., Madigan, M. T., Martinko, J. M., Parker, J. (Eds). 1994. Biology of Microorganisms. Seventh edition, Prentice Hall, NJ. 909 pp
- Brown, S. L., Landry, M. R., Barber, R. T., Campbell, L., Garrison,

- D. L., Gowing, M. M., 1999. Picophytoplankton dynamics and production in the Arabian Sea during 1995 Southwest Monsoon. *Deep Sea Research II*, 46,1745-1768.
- Burkill, P., 1999. ARABESQUE: an overview. *Deep Sea Research II* 46, 529-547.
- Campbell, R.,1983. *Microbial Ecology. Basic Microbiology*, vol. 5, Blackwell Scientific Publications, Oxford (UK). 191
- Carlson, C. A., Bates, N.R., Steinberg, D.K., Hansell, D. A., Johnson, R. J., Knap, A.H., Michaels, A.F., 2000. An overview of biogeochemical variability at the US JGOFS Bermuda Atlantic Time-series Study (BATS) Site. *Ocean Biogeochemistry: A New Paradigm*. pp. 125-126.
- Capone, D. G., 2000. The marine microbial nitrogen cycle pp, 455-494. In: Kirchman, D. L. (Ed), *Microbial Ecology of the Oceans*, Wiley-Liss, Inc, New York
- Chandramohan, D., Ramaiah, N. 1987. Heterotrophic activity and bacterial biomass in coral atolls of Lakshadweep Archipelago. *Contributions in Marine Science*. 117-130
- Cho, B.C. and Azam, F., 1990. Biogeochemical significance of bacterial biomass in the ocean's euphotic zone. *Marine Ecological Progress Series* 63,253-259
- Chrost, R. J., 1990. Microbial ectoenzymes in aquatic environments; In: Overbeck, J., Chrost, R. J. (Eds). *Aquatic microbial ecology: Biochemical and molecular approaches* (New York: Brock/Springer) pp. 47-78.
- Colwell, R. 2000. The future of biocomplexity. *Environmental Microbiology*. 2:3-4.
- Ducklow, H.W., 1993. Bacterioplankton distributions and production in the northwestern Indian Ocean and Gulf of Oman, September 1986. *Deep Sea Research* 40, 753-771.
- Ducklow, H.W., Kirchman, D.L., and Quinby, H.L., 1992. Bacterioplankton cell growth and macromolecular synthesis in sea water cultures during the North Atlantic spring Phytoplankton bloom, May–1989. *Microbial Ecology*, 24, 125-144
- Ducklow H. W., 2000. Bacterial biomass and production in the oceans. pp, 85-120. In: Kirchman, D. L. (Ed), *Microbial Ecology of the Oceans*, Wiley-Liss, Inc, New York
- Ducklow, H.W., Quinby, H. L., Carlson, C. A., 1995. Bacterioplankton dynamics in the equatorial Pacific during the 1992 El Nino. *Deep Sea Research II*, 621-638.
- Ducklow, H. W., Smith, D. C., Campbell, L., Landry, M. R., Quinby, H. L., Steward, G. F., Azam, F., 2001. Heterotrophic bacterioplankton in the Arabian Sea: Basinwide response to year-round high primary productivity. *Deep Sea Research II*, 48,1303-1323.
- Ducklow, H. W., Dickson, M. L., Kirchman, D.L., Steward, G., Orchardo, J., Marra, J., Azam, F., 2000 Constraining bacterial production, conversion efficiency and respiration in the Ross Sea, Antarctica, January-February, 1997. *Deep-Sea Research Part II* 47: 3227-3247.
- Fuhrman, J.A., Ammerman, J.W., Azam, F., 1980. Bacterioplankton in the coastal euphotic zone: distribution, activity and possible relationships with phytoplankton. *Marine Biology*, 60: 201-207
- Fuhrman, J.A., and Azam, F., 1980. Bacterioplankton secondary production estimates for coastal waters of British Columbia, Antarctica and California. *Applied Environmental Microbiology* 39: 1085-1095
- Fuhrman, J.A., and Azam, F., 1982. Thymidine incorporation as a measure of heterotrophic bacterioplankton production in marine surface waters: evaluation and field results. *Marine Biology*, 66: 109-120
- Fuhrman, J.A., Sleeter, T. D., Carlson, C. A., Proctor, L.M., 1989. Dominance of bacterial biomass in the Sargasso Sea and its ecological implications. *Marine Ecology Progress Series* 57: 207-217.
- Gauns, M., 2000. Role of microzooplankton in the foodchain of some tropical marine environments. Ph. D Thesis, Goa University, 210pp.
- Gauthier, M.J. 2000. Environmental parameters associated with the viable but nonculturable state, p. 87-112. In R.R. Colwell, and D.J. Grimes (eds.), *Nonculturable microorganisms in the environment*. ASM Press, Washington D.C.
- Haake, B., Ittekkot, V., Rixen, T., Ramaswamy, V., Nair, R. R., Curry, W. B., 1993. Seasonality and interannual variability of particle fluxes to the deep of the Arabian Sea. *Deep Sea Research* 40, 1323-1344.
- Hansell, D. A., Peltzer, E. T., 1998. Spatial and temporal variations of total organic carbon in the Arabian Sea. *Deep Sea Research* 45, 2171-2194.
- Hobbie, J.E., and Williams, P.J.le B.(eds). 1984. *Heterotrophic Activity in the Sea*: Plenum Press, New York, 569pp.
- Honjo, S., Dymond, J., Warren, P., Ittekkot, V., 1999. Monsoon controlled export fluxes to the interior of the Arabian Sea. *Deep Sea research II* 46, 1859-1902.
- Giovannoni, S.J., Rappe, M.S., 2000. Evolution, diversity, and molecular ecology of Marine prokaryotes. pp, 47-84. In: Kirchman, D. L. (Ed), *Microbial Ecology of the Oceans*, Wiley-Liss, Inc, New York
- Jannasch, H. W., Jones, G. E., 1959. Bacterial Populations in seawater as determined by different methods of enumeration. *Limnology and Oceanography*, Vol. 4, 128-130.
- Jannasch, H. W. 1990. Marine microbiology: A need for deep-sea diving? *Marine Technology Society Journal*, 24: 38-41
- Kemp, P.F., Lee, S. and La Roche, J. 1993. Estimating the growth rate of slowly growing marine bacteria from RNA content *Applied and Environmental Microbiology*, 59: 2594-2601
- Kinne, O. 1980. Diseases of Marine Animals: General Aspects. pp, 13-73. In O. Kinne (Ed.) *Diseases of Marine Animals, Vol. I: General Aspects, Protozoa to Gastropoda*: Wiley, Chichester
- Kirchman, D. L., Rich, J., Barber, R. T., 1995. Biomass and biomass production of heterotrophic bacteria along 140 W in the Equatorial Pacific: effect of temperature on the microbial loop. *Deep Sea Research II* 42: 603-619.
- Kirchman, D. L., Williams, P. J. le B. 2000. Introduction. pp, 1-11. In: Kirchman, D. L. (Ed), *Microbial Ecology of the Oceans*, Wiley-Liss, Inc, New York
- Koga, T. and K. Takumi 1995. Nutrient starvation induces cross protection against heat, osmotic, or H<sub>2</sub>O<sub>2</sub> challenge in *Vibrio parahaemolyticus*. *Microbiology Immunology*, 39: 213-215.
- Kumar, M. D., Sarma, V. V. S. S., Ramaiah, N., Gauns, M., 1998. Biogeochemical significance of transparent exopolymer particles in the Indian Ocean. *Geophysical Research Letters* 25, 81-84.
- Kumar, M. D., Shenoy, D. M., Sarma, V. V. S. S., George, M. D., Dandekar, M., 2002. *Geophysical Research Letters*, 29: 8-11.
- Landry, M. R., 2001. Microbial Loops. In: Steele, J.H., Thorpe, S., Turekian, K.(eds), *Encyclopedia of Ocean Sciences*, Academic Press, London, 1763-1770
- Loka Bharathi, P. A., Nair, S and Chandramohan, D. 2001. Marine microbiology: A glimpse of the strides in the Indian and the global arena, pp 495-537. In: R. Sen Gupta and E. Desa (eds). *The Indian Ocean: A Perspective Vol.1*, Oxford-IBH, New Delhi
- Madhupratap, M., Prasannakumar, S., Bhattathiri, P. M. A., Kumar, M. D., Raghukumar, S., Nair, K. K. C., Ramaiah, N., 1996. Mechanism of the biological response to winter cooling in the northeastern Arabian Sea. *Nature* 384: 549-452.
- Martin, J.H., Coale, K. H., Johnson, K.S., Fitzwater, S.E., Gordon, R. M., Tanner, S.J., Hunter, C.N., Elrod, V.A., Noviwicki, J.L., Coley, T.L., Barber, R.T., Lindley, S., Watson, A.J., Van Scoy, K., Law, C.S., Liddicoat, M.I., Ling, R., Stanton, T., Stockel, J., Collins, C., Anderson, A., Bidigare, R., Ondrusek, M., Latasa, M., Millero, F.J., Lee, K., Yao, W., Zhang, J.Z., Friderich, G., Sakamoto, C., Chavez, F., Buck, K., Kolber, Z., Greene, R., Falkowski, P., Chrisholm, S.W., Hoge, R., Swift, R., Yungel, J., Turner, S., Nightingale, P., Hatton, A., Liss, P., Tindale, N.W., 1994. Testing the iron hypothesis in ecosystems of the equatorial Pacific. *Nature*, 371:123-129
- Menzel, D. W., 1964. The distribution of Dissolved Organic Carbon in the western Indian Ocean. *Deep Sea Research* 11, 757-766
- Nair, R. R., Ittekkot, V., Managani, S. J., Ramaswamy, V., Haake,

- B., Degens, E.T., Desai, B. N., Honjo, S., 1989. Increased particle flux to the deep ocean related to monsoons. *Nature*, 338: 749-751.
- Naqvi, S.W.A., 1994. Denitrification processes in the Arabian Sea. *Proceedings of the Indian Academy of Science* 103, 279-300
- Naqvi S. W. A., 2001. *Chemical Oceanography*. pp.159-236. In: R. Sen Gupta and E. De Sa (eds). *The Indian Ocean: A Perspective* Vol.1, Oxford-IBH, New Delhi
- Naqvi, S.W.A., Noronha, R.J., Reddy, C.V.G. 1982. Denitrification in the Arabian Sea. *Deep- Sea Research*, 29: 459-469.
- Naqvi, S. W. A., Shailaja, M. S., Kumar, M. D., Gupta, R. S., 1996. Respiration rates in subsurface waters of the northern Indian Ocean: Evidence for low decomposition rates of organic matter within the water column in the Bay of Bengal; *Deep Sea Research II* 43: 73-81
- Naqvi S. W. A., Yoshinari, T., Jayakumar, D. A., Altabet, M. A., Narvekar, P. V., Devol, H., Brandes, J. A., Codispoti, L. A., 1998. Budgetary and biogeochemical implication of N<sub>2</sub>O isotope signatures in the Arabian Sea. *Nature* 394: 462-464
- Naqvi S. W. A., Jayakumar, D.A., Narvekar, P.V., Naik, H., Sarma, V.V.S.S., D'Souza, W., Joseph, S., George, M.D., 2000. Increased marine production of N<sub>2</sub>O due to intensifying anoxia on the Indian continental shelf. *Nature* 408: 346-349.
- Paerl, H.W., Prufert- Bebout, L.E., Guo, C., 1994. Iron-stimulated N<sub>2</sub> fixation and growth in natural and cultured populations of the planktonic marine cyanobacteria *Trichodesmium* spp. *Applied and Environmental Microbiology*, 60:1044-1047.
- Paerl, H. W., Zehr, J. P. 2000. Marine nitrogen fixation pp 387-426. In: Kirchman, D. L. (Ed)., *Microbial Ecology of the Oceans*, Wiley-Liss, Inc, New York
- Pomeroy, L. R., 1984. Microbial processes in the sea: diversity in nature and science. pp 1-25. In: Hobbie, J. E and Williams, P.J. leB. (eds). *Heterotrophic Activity in the Sea*. Plenum Press New York 569 pp
- Pomeroy, L. R., Macko, S. A. Ostrom, P.H., Dunphy, J., 1990. The microbial food web in Arctic seawater: Concentration of dissolved free amino acids and bacterial abundance and activity in the Arctic Ocean and in Resolute Passage. *Marine Ecology Progress Series*, 61: 31-40.
- Pomroy, A. J., Joint, I. R., 1999. Bacterioplankton activity in the surface waters of the Arabian Sea during and after the 1994 SW monsoon. *Deep Sea Research II* 46:767-794
- Prasannakumar, S., Ramaiah, N., Gauns, M., Sarma, V.V.S.S., Muraleedharan, P. M., Raghukumar, S., Kumar, D. M., Madhupratap, M. 2001. Physical forcing of biological productivity in the Northern Arabian Sea during the Northeast Monsoon. *Deep-Sea Research II* 48: 1115-1126
- Ramaiah, N. 1989. Studies on marine luminous bacteria. Ph D Thesis, Rani Durgavati University. 230p
- Ramaiah, N., Raghukumar, S., Gauns, M. 1996. Bacterial abundance and production in the central and eastern Arabian Sea. *Current Science* 71: 878-882.
- Ramaiah, N., Sarma, V.V.S.S., Gauns, M., Kumar M.D., Madhupratap, M., 2000. Abundance and Relationship of bacteria with transparent exopolymer particles during the 1996 summer monsoon in the Arabian Sea. *Proceedings of the Indian Academy of Sciences (Earth and Planetary Science)* 109: 443-451.
- Rao, V.P.; Michard, A.; Naqvi, S.W.A.; Boettcher, M.E.; Krishnaswamy, R.; Thamban, M.; Natarajan, R.; Borole, D.V. 2002. Quaternary phosphorites off the southeast coast of India *Chemical Geology* 182: 483-502
- Roberts, R.D., Zohary, T. 1993. Fact or fiction- bacterial growth rates and production as determined by methyl- <sup>3</sup>H-thymidine? *Advances in Microbial Ecology*. 13: 371-425
- Sarma, V. V. S. S., Swathi, P. S., Kumar, M. D., Prasanna Kumar, S., Madhupratap, M., Ramaswamy, V., Sarin, M. M., Gauns, M., Ramaiah, N., Sardesai, S., de Souza S. N., 2003. Carbon budgets for the JGOFS (India) study region in the Arabian Sea. *Global Biogeochemical Cycles*. 13: 17-33
- Sherr, E., Sherr, B., 2000. Marine microbes: an overview. pp, 13-46. In: Kirchman, D. L. (Ed)., *Microbial Ecology of the Oceans*, Wiley-Liss, Inc, New York
- Shetye, S.R.; Gouveia, A.D.; Shenoi, S.S.C., 1994. Circulation and water masses of the Arabian Sea pp: 107-123. In: Lal, D (Ed) *Biogeochemistry of the Arabian Sea: Present information and gaps*, Indian Acad. of Sciences, Bangalore, India.
- Singleton I, Megharaj M, Kantachote D, Naidu R. 2000. Effect of long-term contamination of DDT on soil microflora with special reference to soil algae and algal transformation of DDT. *Environmental Pollution*, 109: 35-42
- Smith, D. C., Steward, G. F., Long, R. A., Azam, F., 1995. Bacterial mediation of carbon fluxes during a diatom bloom in a mesocosm. *Deep Sea Research* 42, 75-98.
- Smith, S. L., Codispoti, L. A., Morrison, J.M., Barber, R. T., 1998. The 1994-1996 Arabian Sea Expedition: an integrated interdisciplinary investigation of the northeastern Indian Ocean to monsoonal forcing. *Deep Sea Research II*, 45, 1905-1915.
- Steele, J.H., Thorpe, S., Turekian, K. (eds), *Encyclopedia of Ocean Sciences*, Academic Press, London.
- Strom, S.L., 2000. Bacterivory: interactions between bacteria and their grazers. pp 351-386. In: Kirchmann, D.L.(ed), *Microbial ecology of the oceans*. Wiley-Liss, New York
- Swallow, J. C., 1984. Some aspects of the physical oceanography of the Indian Ocean. *Deep Sea Research* 31, 639-650.
- Takahashi, K. 1986. Seasonal fluxes of pelagic diatoms in the subarctic Pacific, 1982-1983. *Deep Sea Research* 33, 1225-1251.
- Warren, B. A., 1994. Context of the suboxic layer in the Arabian sea. In: Lal, D. (Ed.). *Indian Academy of Sciences, Bangalore, India*, pp.203-216.
- Wiebinga, C. J., Veldhuis, M. J. W., De-Baar, H. J. W., 1997. Abundance and productivity of bacterioplankton in relation to seasonal upwelling in the northwest Indian Ocean. *Deep Sea Research* 14: 451-476.
- Winn, C.D., Karl, D. M. 1984. Microbial productivity and community growth rate estimates in the Tropical North Pacific Ocean. *Biological Oceanography*, 3:123-145.
- Zilinskis, R. A., Colwell, R. R., Lipton, D. W., Hill, R. T. 1995. *The Global Challenge of Marine Biotechnology*. Maryland Sea Grant, College Park, MD, 298 p