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## Ecology and biology of luminous bacteria in the Arabian Sea

N. RAMAIAH and D. CHANDRAMOHAN

National Institute of Oceanography, Dona Paula, Goa - 403 004, India

**Abstract**-Extensive studies on occurrence, distribution and species composition of luminous bacteria in the Arabian Sea were carried out from various habitats such as water (up to 1000 m), sediment, suspended particles, zooplankton, seaweeds, benthos, digestive tracts and light organs of fishes. Luminous bacterial population was by far the highest in the environs of the Arabian Sea. Their distribution pattern was of free-living nature in coastal, lagoon and upper 200m of oceanic regions. Their numbers were low in the oligotrophic equatorial waters. *Vibrio harveyi*, *V. fischeri*, *Photobacterium leiognathi* and *P. phosphoreum* were the luminous species found to occupy various niches. *V. harveyi* showed a greater ecological versatility, *V. fischeri*, a remarkable ecological adaptation and *P. leiognathi* occurred mostly as light organ symbiont in leiognathid fishes. *P. phosphoreum* was recorded from the water column with temperatures lower than 25°C. Bacterial luminescence in all the seawater samples was very low indicating energy conservation mechanism in free-living luminous prokaryotes. In contrast, a 10000 fold higher bacterial luminescence was observed from all the examined zooplankton samples implying an abundance of surface associated luminous microflora and a continuous luciferase synthesis. Suppression of luminescence in primary isolates collected from coastal environs receiving toxic materials was seen. Information on their ecology from the Arabian Sea is discussed in terms of their use in quicker assessment of environmental stresses, in the environmental monitoring programmes, biological watermass characterisation, upwelling and other processes.

### INTRODUCTION

Knowledge of marine microbial ecology is a fundamental requirement for understanding biological processes in the oceans. Microbial activities play an important role in marine foodwebs, nutrient mineralization and recycling. Information on the taxonomically well defined groups of microorganisms help in assessing marine microbial processes (KARL, 1986). Of several such groups suitable for ecological studies, luminous bacteria offer several advantages. They are truly marine, occupy a variety of ecological niches, enjoy more than one life-style (namely free living and symbiotic). Also, they are easily recognisable by the virtue of their luminescence, easily culturable and a well defined taxonomic scheme is available (REICHELDT and BAUMANN, 1973) for unambiguous and routine identification purposes. As far as their ecological activities are concerned, they are like any other heterotrophic bacteria and are known to utilize a variety of nutrients in the sea (CHUMAKOVA and GETELSON, 1975). They are found to be distributed from surface to several thousands of metres (RUBY *et al* 1980) as free living, parasitic, saprophytic and as light organ symbionts (HASTINGS *et al* 1987).

Ecology of bioluminescent bacteria has focussed primarily on establishing the distribution and importance of these organisms in the marine environment (NEALSON and HASTINGS, 1979). Microbiological studies in the Atlantic and Pacific oceans have been directed towards the quantitative and qualitative distribution of these bacteria in different oceanic regimes (RUBY and NEALSON, 1978; O'BRIEN and SIZEMORE, 1979; YETINSON and SHILO, 1979; ORNDORFF and COLWELL, 1980; FELDMAN and BUCK, 1984 and VENKATESWARAN *et al*, 1989).

The Indian Ocean is considered the richest source of bioluminescent organisms (LYNCH, 1981). Studies on planktonic bioluminescence in and around a "milky sea"

in the western Arabian Sea have ascertained that the particle colonising luminous bacterium, *Vibrio harveyi* and other luminescent dinoflagellates, euphausiids and copepods are the cause of the reported bioluminescence (LAPOTA *et al* 1988). In spite of the fact that a wide range of habitats are occupied by luminous bacteria, very little information concerning their ecology, distribution, occurrence and species composition is available for the Indian Ocean. Earlier studies have documented their occurrence in the nearshore waters (NAIR *et al* 1979; JAYABALAN *et al* 1982 and RAMESH *et al* 1987). Examination of different habitats in the Arabian Sea has largely been neglected (LAKSHMANAPERUMALSAMY *et al* 1981). In our earlier studies (RAMAIAH and CHANDRAMOHAN 1987, 1988), we have reported their distribution pattern in different regions in the coastal and oceanic waters. Their association with different ecological niches as well as their physiology were examined in greater detail in a recent study (RAMAIAH, 1989). The present paper reports biological and ecological aspects of luminous bacteria occurring as free living forms in the water column in different oceanic regimes and of those inhabiting in specific and nonspecific associations among various available ecological niches in the Arabian Sea.

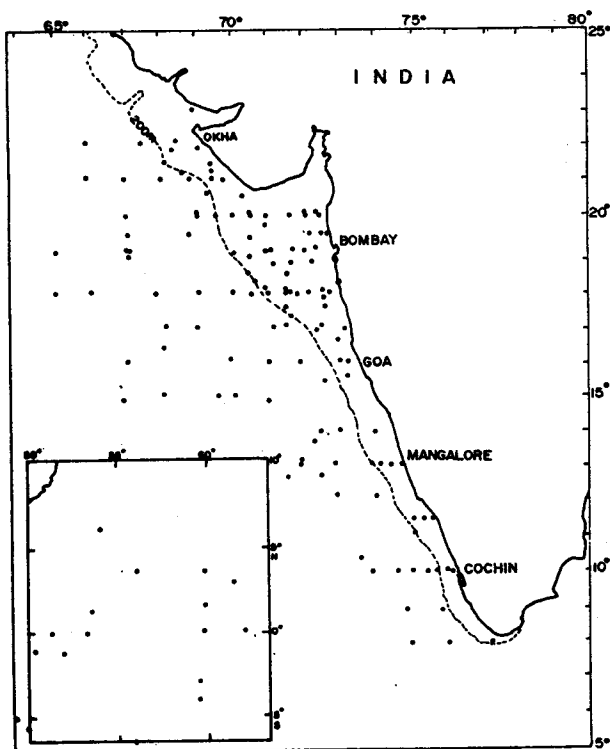


Fig.1. Sampling stations (stations within 200m contour are considered coastal; outside ones oceanic and inset oligotrophic).

## MATERIALS AND METHODS

Distribution of platable populations of aerobic, heterotrophic as well as that of luminous procaryotes from various habitats was studied for a period of five years during 1985-89. Water samples from coastal, lagoon and oceanic regions were collected and analysed during 12 different oceanographic cruises, and monthly samples were

collected from the Dona Paula Bay (estuarine condition) for over one year. Sampling locations for this study are shown in Fig.1. Samples from different depths were collected by using either Johnson-Zobell bacteriological sampler or Niskin's sterile bag samplers. Various other ecological niches examined for the occurrence and distribution of luminous bacteria include suspended particles, sediments, sessile and other benthic organisms, gut contents of fishes and bivalves, surfaces of seaweeds and zooplankters as well as the light glands of leignathids.

Seawater complete (SWC) agar medium containing peptone 5.0 g yeast extract 3.0 g glycerol 3.0 ml, agar 15.0 g, aged seawater 750 ml and distilled water 250 ml was used for the enumeration of total viable heterotrophic bacterial populations. Membrane filtration (0.22  $\mu\text{m}$  Millipore Inc., USA) was used to sample water and suspended particles; serial dilution and spread plate techniques were used for all other samples for enumeration of viable bacteria. Standard microbiological methods were followed for incubation, enumeration, isolation and purification of luminous procaryotes (NEALSON, 1978). Most of the luminous colonies were picked up for further studies, from those samples which had low counts of these colonies. Purified strains of these isolates were then subjected to biochemical characterization following the criteria laid down by REICHELTL and BAUMANN (1973).

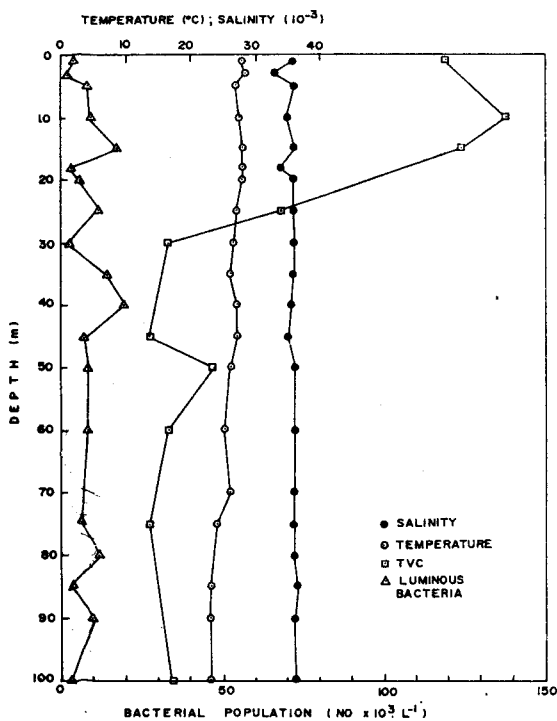


Fig.2. Distribution of various parameters in the coastal waters (mean values of all coastal stations)

Bioluminescence of seawater was measured following a method similar to the one described by NEALSON *et al* (1984). Details of the procedure followed are published elsewhere (RAMAIAH and CHANDRAMOHAN, 1988). Bioluminescence due to luminous bacteria associated with zooplankton was also measured in order to see

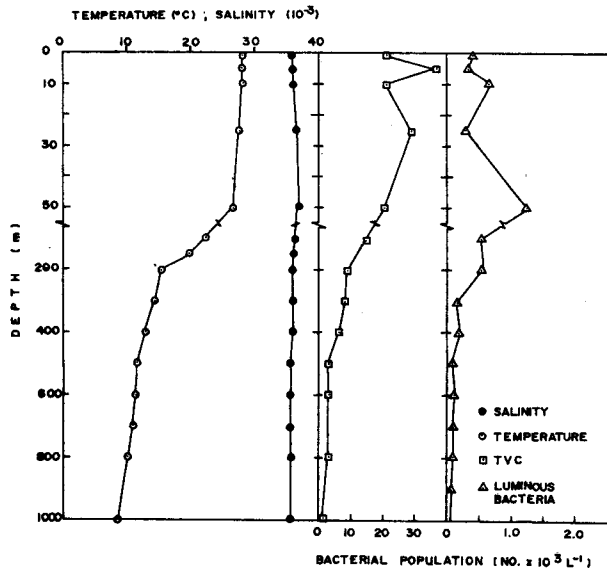


Fig.3. Distribution of various parameters in the oceanic waters (mean values of all oceanic samples)

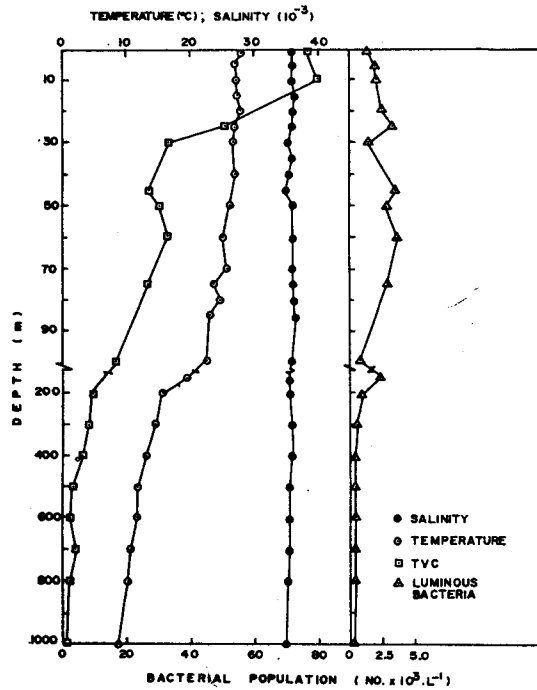


Fig.4. Distribution of various parameters in the Arabian Sea (mean values of both coastal and oceanic samples)

whether or not the natural luminous microflora associated with animal surfaces emit light, and, if luminescing, to what extent.

## RESULTS

In order to examine the overall distribution pattern of luminous as well as general heterotrophic bacterial populations in the Arabian Sea, a total of 516 water samples collected from various depths were analysed. Of these, 300 samples were from the oceanic region and the rest from the coastal ( water column depth less than 200m ) region. Mean numbers of luminous bacteria in the coastal waters are far greater than those recorded from the oceanic areas ranging from  $0.78 \pm 0.3$  (SD)  $\times 10^3$  to  $14.38 \pm 1.87 \times 10^3$  cells in the coastal and from  $0.041 \pm 0.006$  to  $3.47 \pm 1.59 \times 10^3$  cells  $L^{-1}$  in the oceanic samples. When the data from all the sampling stations were compared, it was evident that the heterotrophic bacterial populations fluctuated widely both in the coastal and oceanic (Figs.2,3) waters without showing any geographic or seasonal differences. Nonetheless, an overall decrease in TVC with increasing depth was discernible. A highly fluctuating trend in the abundance of luminous bacteria was seen in the upper 50 m unlike in the deeper waters (Fig. 4). Simple correlation coefficient (r) values as suggested by ORNDORFF and COLWELL (1980) were calculated to find out the pattern of distribution of luminous bacterial populations. These r values confirm the TVC - dependent distribution of luminous bacteria in the entire water column in the coastal region (Table 1). Whereas, such TVC dependent distribution was evident only in the upper 200 m in the oceanic region (Table 1). In the lagoons of the Lakshadweep islands (Table 2), though the luminous bacteria constituted a small (2.70 to 6.30%) fraction of viable bacterial populations ( $2.40 \times 10^5$  to  $7.66 \times 10^5$  cells  $L^{-1}$ ), in terms of numbers, they were far greater ( $1.5$  to  $45 \times 10^3$  cells  $L^{-1}$ ) than those recorded from coastal or oceanic waters. Also, a very high correlation existed between TVC and luminous bacteria ( $r = 0.879$ ) signifying their free living pattern. Besides indicating a year round abundance (Fig. 5), luminous cell counts ( $9.0$  to  $58.33$  cells  $L^{-1}$ ) recorded from the monsoon and freshwater influenced Dona Paula Bay are by far the highest, contributing roughly to about 5 to 20% of TVC. Generally, higher counts of luminous bacteria were recorded during the post monsoon months.

Table 1. Correlation coefficient values between bioluminescent bacteria and total viable bacterial populations in the coastal and oceanic waters

depth(m)	no. of coastal samples		depth(m)	no. of oceanic samples	
1	61	0.529	1	46	0.447
3	8	0.972	5	12	-0.503
5	11	0.676	10	33	0.427
10	33	0.625	25	12	-0.532
15	7	0.663	50	24	0.583
18	7	0.559	100	59	0.502
20	10	0.489	150	7	0.950
25	17	0.611	200	39	0.867
30	8	0.549	300	7	0.336
40	9	0.805	400	5	0.176
45	6	0.996	500	15	0.261
50	15	0.641	600	5	0.112
60	6	0.643	700	3	0.326
70	6	0.961	800	5	0.234
75	12	0.712	1000	10	0.269
80	4	0.987			
90	6	0.999			
100	8	0.953			

All the "r" values for the coastal samples statistically significant at 1 or 5% level of significance. Such significance was not found for oceanic samples below 300 m.

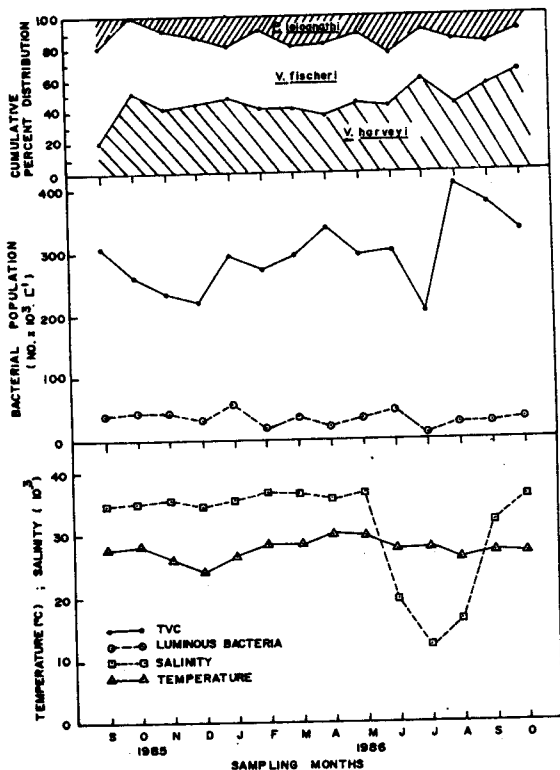


Fig.5. Seasonal variations of different parameters in Dona Paula Bay

Fig.6 summarises, the distribution pattern of luminous bacteria in different habitats. It can be seen from this figure that particle associated luminous bacteria form an important portion constituting nearly 15% of attached bacteria. They were found in association with copepods, ostracods, fish larvae, euphausiids and other crustaceans. None of the amphipods, pteropods or polychaetes were found to harbour luminous bacteria. Sediment samples were found to harbour low counts of luminous bacteria irrespective of their geographic origin. Similarly, they were a very minor component of the epiphytic microflora on 7 of the 8 species of seaweeds examined. Guts of the green mussel, *Perna viridis*, always harboured higher numbers of luminous bacteria which showed a very high correlation ( $r = 0.943$ ) with TVC. Luminous bacteria were present in the guts of all the species of fishes examined constituting anywhere from 2.49 to 16.67% of TVC. *Photobacterium leiognathi* was the sole bacterium in the light glands of 5 species of leiognathids with its number ranging from  $9.75 \times 10^9$  to  $90.00 \times 10^9$  cells  $g^{-1}$  wet wt. of the gland.

*V. fischeri* and *V. harveyi* were found to be the dominant species (Fig.7) in the oceanic waters. Together they accounted for over 65% of the total luminous strains. *V. harveyi* was found to occur up to 500 m, and below this depth only *V. fischeri* and *P. phosphoreum* were obtained. Occurrence of *P. phosphoreum* was found from depths below 100m. Strains of *P. leiognathi* were scarce in the collections. Nonetheless, vertical distribution of this species was similar to that of *V. harveyi*. In the coastal waters, *V. fischeri* constituted 44% of 256 luminous strains, *V. harveyi* 36%, *P. leiognathi* 16% and *P. phosphoreum*, isolated from depths below 85 m and temperatures lower than  $25^\circ\text{C}$ , accounted only for 4% of the luminous isolates collected from this region. In Dona

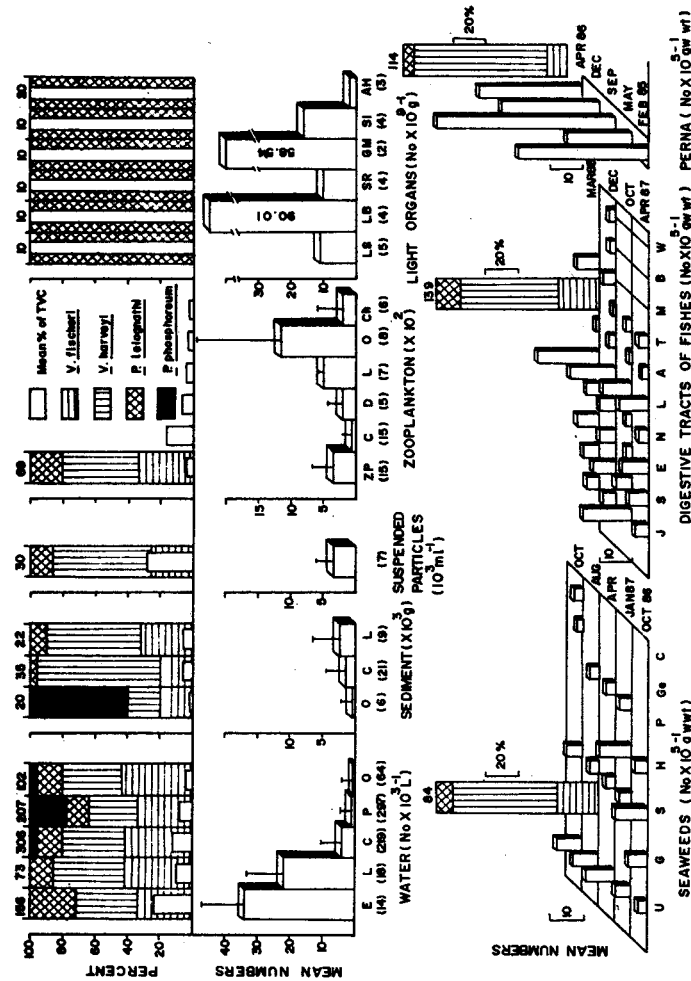


Fig. 6. Mean numbers and percentage contribution of luminous bacteria in different types of habitats. Figures in the parentheses indicate number of samples collected and examined from various sources. Figures on top of the histograms indicate numbers of luminous isolates characterised to arrive at the species composition. The mean numbers of luminous bacteria from different sources such as water, sediment and others are given on the y axis, but the units per litre or per gram sediment are given in the parentheses on the x axis. Abbreviations under water and sediment are, E- estuarine, L- lagoon, C- coastal, P- pelagic (oceanic) and O- oligotrophic. Abbreviations under zooplankton: ZP- zooplankton (assorted sample), C- copepods, D- decapods, L- lucifers, O- ostracods and Ch- chaetognaths. Abbreviations under light organs: LS- *Leiognathus splendens*, LB- *L. brividus*, SR- *Secutor rucomis*, SI- *S. insidiator*, GM- *Gazza minuta* and AH- *Antennarius hispidus*. Abbreviations under sea weeds: U- *Ulva* sp, G- *Gracillaria* sp, S- *Sargassum* sp, H- *Hymnea* sp, C- *Celidium* sp and C- *Chaetomorpha* sp. Abbreviations under digestive tracts of fishes: J- *Johnius dussumieri*, S- *Sardinella longiceps*, E- *Engraulis dussumieri*, N- *Nemipterus japonicus*, L- *Leiognathus splendens*, A- *Ambassis* sp, T- *Trichurus* sp, M- *Mugil* sp, B- Ballistid fish (trigger fish) and W- Wrasse (Halichoeridae).

Paula bay, unlike in the coastal and oceanic waters, there was a dominance of *V. harveyi* (45%) over *V. fischeri* (Fig. 5). *P. leiognathi* was a minor component and showed a patchy occurrence in this bay. A similar distribution pattern was seen in the lagoon waters also (Table 2). *V. harveyi* was the most dominant species in all the nonspecific associations such as coastal sediments, digestive tracts, suspended particles, surfaces of zooplankters and seaweeds (Fig. 6). *P. leiognathi* was the light organ specific symbiont in leiognathids and in the bait organ of *Antennarius hispidus*, which is a new record.

Very low values of bioluminescence of seawater were recorded and it ranged from undetectable levels to  $2.5 \times 10^{-2}$  light units, from 0 to  $8 \times 10^{-2}$  and from 0 to  $12.5 \times 10^{-2}$  light units in oceanic, coastal and lagoon waters respectively. Luminous bacteria were present in varying numbers in many of the samples from which no luminescence was recorded and a negative relationship existed between luminous bacterial numbers and the seawater bioluminescence (light units) values. On the contrary, zooplankton filtrates had very high bioluminescence values ranging from 58.50 to 92.86 light units, which is about 5 order of magnitude higher than that was recorded for seawater samples. The decrease in the light levels measured at regular intervals from the filtrates showed that this bioluminescence was of bacterial origin.

Table 2. Distribution of total viable counts and luminous bacteria in the lagoon waters of Lakshadweep islands

Station	TVC	LB	LB%	species composition		
				1	2	3
Kavaratti (1985)	732	21	2.87	2*	2	1
	714	45	6.30	1	2	1
	626	19	3.04	2	2	1
Kavaratti (1987)	370	10	2.70	2	2	1
	395	15	3.80	1	1	1
	330	20	6.06	3	0	0
Agatti (1985)	423	13	3.07	1	1	2
	410	16	3.90	2	2	1
	355	18	5.10	2	1	1
	168	5	2.98	1	2	2
	602	25	4.15	2	1	1
	713	36	5.05	1	1	1
	654	26	3.98	2	1	1
Bingaram (1985)	737	35	4.75	1	2	2
	766	41	5.35	3	1	1
Kadmat (1987)	500	15	3.00	2	1	0
	390	15	3.85	1	1	1
	240	15	6.25	1	2	0

TVC = Total Viable Counts (no.  $\times 10^3 L^{-1}$ ), LB = Luminous bacteria (no.  $\times 10^3 L^{-1}$ ), 1 = *V. harveyi*, 2 = *V. fischeri*, 3 = *P. leiognathi*, \* = number of isolates.

## DISCUSSION

Luminous bacteria exist in planktonic or freeliving state as part of the general microbial population performing the well known heterotrophic function of deriving energy for growth from organic nutrients and, in this process, mineralizing these nutrients through their biodegradative mechanisms. The present study on the distribution of luminous procaryotes, was aimed at examining the distribution pattern of this taxonomically well defined group as intensively as possible. Generally, waters of the Arabian Sea were found to sustain more luminescent bacteria than any other



part of the world oceans from which luminous procaryote distribution has been recorded. The shelf region in the west coast of India is very rich in terms of their abundance (RUBY and NEALSON, 1978; YETINSON and SHILO, 1979) which is comparable to the highly productive estuarine regions (O'BRIEN and SIZEMORE, 1979; FELDMAN and BUCK, 1984; RAMESH *et al* 1987). Lower counts of these bacteria were recorded from the oceanic waters. These counts are much higher than the planktonic luminous bacteria enumerated from the Puerto Rican coast (RUBY *et al* 1980) and from the Pacific Ocean (VENKATESWARAN *et al* 1989). Luminous and general bacterial counts were far lower in the equatorial regions (Fig. 1 inset) than those recorded from the oligotrophic Sargasso Sea (ORNDORFF and COLWELL, 1980).

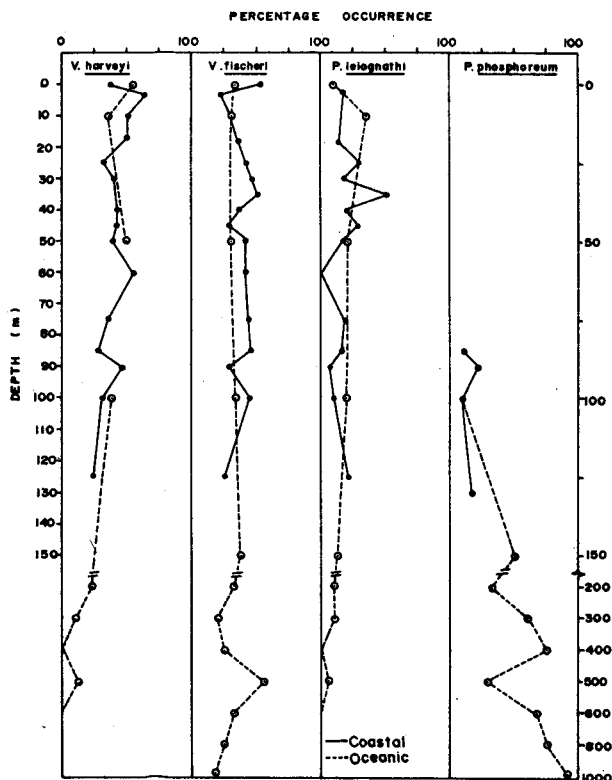


Fig.7. Species composition of luminescent bacteria in the water column (based on all samples from various stations shown in figure 1)

Interestingly, nutrient concentrations in this area are also very very low (ANON, 1971). RUBY and NEALSON (1978) and CHUMAKOVA and GETELSON (1975) have indicated that the occurrence of higher numbers of luminous bacteria is a positive indication of higher nutrient concentrations. QASIM (1982) has reviewed the oceanography of the Northern Arabian Sea. Based on the data from 166 stations covering coastal and oceanic regions, he concluded that the primary production in the coastal waters (shelf region) is at least 3.5 times higher than that in the offshore (oceanic) waters. It was also highlighted in this review that the coastal areas in the Arabian Sea are among the most productive areas of the world oceans. Observations on the

distribution pattern of luminous bacteria in the Arabian Sea were compared with primary production data (QASIM, 1982). Table 3 indicates that clear cut demarkation of highly productive coastal, poorly productive oceanic and oligotrophic equatorial waters is possible by monitoring a taxonomically well defined group such as luminous bacteria. Observations on the occurrence, abundance and species composition of luminous procaryotes from specialised environment such as coral reef lagoons are not available. Highly active microbial (LOKABHARATHI *et al* 1986; CHANDRAMOHAN and RAMAIAH, 1987; RAGHUKUMAR *et al* 1987) and phytoplankton communities (QASIM *et al* 1972) contributing to highly productive lagoon ecosystems situated amidst nutrient deficient oceanic region have been reported. Observations of the present study also indicate the highly productive nature of the coral reef ecosystems (Tables, 2 and 3).

Table 3. Comparative account on the primary production, nutrients and bacterial populations in different regimes of the Arabian Sea

parameter	estuarine <sup>a</sup>	lagoon <sup>b</sup>	coastal <sup>c</sup>	oceanic <sup>c</sup>
Chl a <sup>d</sup>	5.0	0.17	0.80	0.26
Pri. prod(s) <sup>e</sup> (euphot)	<50-1000 500->16000	0.51-2.49 -	50->100 1-> 2	<10-25 <0.5-0.5
NO <sub>3</sub> -N <sup>f</sup>	0.2-8.2	0.1-1.1	2.5-> 5	< 2.5
PO <sub>4</sub> -P <sup>g</sup>	0.1-4.5	0.1-0.5	1.5-> 7.5	< 0.5
av.pri. prod <sup>h</sup>	43.21	12.90	37.45	10.51
TVC <sup>i</sup>	203-405	240-766	34-138	9-77
lum.bacteria <sup>j</sup>	9- 58	10- 45	0.8- 14	0.04- 3.5

a = Devassy and Goes (1989), b = Qasim *et al* (1972) c = Qasim (1982), d - expressed as mg m<sup>-2</sup>, e - as mg C m<sup>-3</sup>d<sup>-1</sup> under ref. a,b and c (a factor of 10 is used to convert the original values to mg C m<sup>-3</sup>d<sup>-1</sup> from mg C m<sup>-3</sup>h<sup>-1</sup> under ref.a), f and g = µg. at L<sup>-1</sup>, h - expressed as mg C m<sup>-2</sup> under ref. a and as mg C m<sup>-3</sup>d<sup>-1</sup> under ref. b and c, i = total viable bacteria(no. ml<sup>-1</sup>) j = luminous bacteria (no. ml<sup>-1</sup>), euphot = euphotic zone, s = surface

Counts of luminous bacterial populations recorded from the Dona Paula Bay are the highest observed compared with any part of the world oceans. Neither salinity nor temperature seemed to influence their distribution pattern. Extensive studies in the Mandovi-Zuari estuarine system of Goa (DEHADRAI and BHARGAVA, 1972; SHAILAJA and PANT, 1986) have revealed that this estuarine system sustains high primary production, high nutrient levels and high secondary production and there are low variations in seasonal temperature and oxygen concentrations. This bay is reported to be apparently free from eutrophication (DEVASSY and GOES, 1989) owing to rapid turnover of nutrients by the biologically highly active communities. Besides substantiating higher biological productivity, higher densities of luminous bacteria in this bay also signify pollution free environs in this estuarine complex.

Examination of various other types of samples including suspended particles, sediments and gut contents confirmed the ecological versatility of these procaryotes. They seem to colonise body surfaces of zooplankters having chitin as the chief exoskeletal constituent. The preferred niche of this group in the nutrient impoverished oligotrophic waters appears to be the gut and body surfaces of zooplankton. Although the role of attached and free living bacteria needs to be clearly elucidated (AZAM, 1983), a substantial percentage of luminous procaryotes exist in attached mode.

Enteric luminous bacterial flora has the advantage of deriving its energy from this protected and nutritionally rich niche. These bacteria may help in the breakdown of food particles (eg. chitinous material) that can then be easily assimilated by the

animal. Upon deriving energy through such activities, these bacteria grow and multiply rapidly. Shedding or release through feces, body surfaces, may contribute to the free living luminous microflora which later colonise particles, feces, caracases of microzooplankton etc. and the emission of light by these attached bacteria may attract a potential feeder to feed on these particles thus enhancing their chances of reentry into the ecologically more advantageous niche. This might explain the functional role of bioluminescence in these procaryotes (NEALSON and HASTINGS, 1979). Free living luminous bacteria in the water column may, therefore, act as a reservoir of cells received through and donated to specific (light organ symbiosis) and non-specific (enteric, particle attached, epiphytic etc.) associations.

Measurements of seawater bioluminescence imply a natural tendency of luminous bacteria to conserve energy while existing in planktonic form. While in association - whether specific or nonspecific - with marine animals or suspended particles (ANDREWS *et al* 1984), they keep emitting light. As is evident from the recent work of MAKEMSON and GORDON (1989), 12% of the oxygen respired goes into the bioluminescence pathway and this energy consuming reaction has no functional advantage in the free living bacteria. Whereas, those colonising plankton surfaces, feces and particles, if emitting light which is usually at the cost of the colonised substratum, can enhance their chances of entering an ecologically more advantageous niche.

Although strains belonging to luminous genera were recovered, luminous colonies were absent in all the 85 water and 24 sediment samples collected from the Bombay Harbour, Thana Creek, Bassein Mouth and Amba River estuary. These areas receive significant amounts of industrial and urban wastes. These observations signify the sensitivity of bacterial luminescence to toxic materials. Therefore, monitoring for bioluminescent bacteria may aid in the quick assessment of environmental health.

Luminous bacteria serve as valuable tools for biological watermass characterization (YETINSON and SHILO, 1979). Data on the quantitative distribution of bioluminescence and total bacterial numbers were found to be positively correlated (GORDENKO *et al* 1980) and helpful in assessing primary productivity in the ocean (TOKAREV *et al* 1985). Differential distribution pattern of luminous procaryotes in different regions of the Arabian Sea compare quite well with that of the data on primary productivity. Occurrence of psychrotrophic *P. phosphoreum* as noted during this study in the surface layers in the coastal regions of the tropical waters can serve as an aid in assessing the presence of upwelled waters. Ecological studies on this taxonomically well defined group can, therefore, be useful in the detection of biological water structures.

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