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Physiological Characteristics Underlying the Distribution Patterns of Luminous Bacteria in the Mediterranean Sea and the Gulf of Elat

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Physiological characteristics of luminous bacteria isolated from the Mediterranean and Gulf of Elat were compared to determine their relationship to the specific seasonal and geographic distribution patterns of these bacteria. The effects of temperature on growth rate and yield, relative sensitivity to photooxidation, resistance to high salt concentration (8%), and ability to grow in nutrient-poor conditions appear to control these patterns. The winter appearance of *Photobacterium fischeri* and the succession of winter and summer types of *Beneckea harveyi* in the eastern Mediterranean are explained by different temperature requirements for growth. Sensitivity to photooxidation explains the disappearance of *P. leiognathi*, present in the main body of the Gulf of Elat throughout the year, from the shallow coastal strip. *B. harveyi* is present in this coastal strip which is higher in nutrients and in productivity than the open waters. Competition experiments between *B. harveyi* and *P. leiognathi* in batch and continuous culture indicate that the oligotrophic *P. leiognathi* is outcompeted by *B. harveyi* in rich and even in relatively poor media. The distribution pattern found in the Bardawil hypersaline lagoon is explained by selection of salinity-resistant mutants of *B. harveyi* from the Mediterranean Sea.

Luminous marine bacteria show a characteristic geographic and seasonal distribution pattern. This was recognized as early as 1889 by Beijerinck (4, 5), who described the seasonal fluctuation of luminous bacteria of the North Sea where *Bacillus phosphoreum* (syn., *Photobacterium phosphoreum*), dominant throughout the entire year, was partially replaced in the summer months of August and September by *P. splendidum* (syn., *Beneckea harveyi* or *B. splendida*). A different seasonal distribution pattern has been described recently from the southern California coast of the Pacific Ocean (20) where *P. fischeri*, present throughout the year, was partially replaced by *B. harveyi* during the summer. In autumn and in winter, *P. phosphoreum* was an additional minor component of this luminous bacterial community. Another fluctuation pattern was found in the eastern Mediterranean (M. Shelubsky-Shilo, M.S. thesis, Hebrew University of Jerusalem, 1943), where several types of *B. harveyi* occur in sequence during the year and where an intrusion of a different type of luminous bacterium, now recognized as *P. fischeri*, takes place in the winter. In a previous paper (23) we described the distribution pattern of different luminous bacterial types in the eastern Mediterranean and the Gulf of Elat: *P. fischeri*, a typical Mediterranean winter type, is absent from the Gulf of Elat, whereas the Gulf of Elat species, *P. leiognathi*, is never found in eastern Mediterranean waters. Seasonal differences in *B. harveyi* strains were marked in the coastal region of the Mediterranean Sea. *B. harveyi* was the dominant species in the shallow coastal strip of the Gulf of Elat; however, it was not isolated from deeper open waters of the gulf. In the present paper, we consider whether the physiological characteristics of the different luminous bacterial types can explain their geographic and seasonal patterns, and we evaluate the role of specific environmental factors in governing their distribution.

Ecological conditions for single environmental factors such as temperature, light, and nutrient and salt concentrations were simulated experimentally to determine their effect on pure cultures of luminous bacteria. The findings were related to the observed population dynamics of luminous bacteria (23).

MATERIALS AND METHODS

Bacterial strains and cultivation conditions. *B. harveyi*, *P. leiognathi*, and *P. fischeri* isolates from

the Mediterranean Sea, the hypersaline Bardawil lagoon, and the Gulf of Elat were compared (23). For growth of the bacteria, yeast extract-peptone medium (YP) and basal medium containing 3 or 8% NaCl was used (23). The same media with 1.5% Difco agar served for plating.

Photooxidation experiments. Luminous bacteria were grown in a shaker on YP medium (3% NaCl) at 26°C, harvested by centrifugation (15 min at 10,000 × *g*), and suspended in sterile seawater. Laboratory experiments on photooxidation were carried out by using a Widioscope (AB Wiktoks Mekaniska, Jarfalla, Sweden), with a halogen lamp (250 W, 24 V) as the light source. These photooxidation experiments were carried out in sealed, flat-bottom tubes 1 cm in diameter, at a light intensity of 10^6 ergs·cm^{-2}·s^{-1}. The suspensions were kept in an atmosphere of pure O_2 at 25°C, with continuous stirring by a magnetic stirrer. In the experiments where a photosensitizer, toluidine blue (1 μM), was added, the light source was an illuminated Warburg monometer unit with tungsten lamps (40 W, 220 V) (B. Braun Melsungen AG, W. Germany).

In situ experiments to detect photodynamic damage were carried out at station 3 (23) in the Gulf of Elat. Different strains of luminous bacteria were placed in cellophane dialysis tubes, 1 cm in diameter, and suspended in different depths of the water column as previously described (1, 9). A parallel series of cellophane tubes covered by black plastic sheets served as controls.

SOD activity determination. Cells were harvested, suspended in 0.01 M potassium phosphate at pH 7.8, and disrupted for 30 s with glass beads (0.10 to 0.11 mm in diameter) in a Nossal Homogenizer (Case Western Reserve University, Cleveland, Ohio). Cell debris was removed by centrifugation at 30,000 × *g* for 15 min, and the cell-free extracts used for the enzyme assay were obtained by the procedure of McCord and Fridovich (15). Protein was determined by the method of Davis (8); at 4°C at a current of 3 mA per gel cylinder, superoxide dismutase (SOD) activity was localized by the negative staining procedure described by Beauchamp and Fridovich (3). The gels were scanned at 560 mm.

Transfer of bacteria from low to high salt concentration. Transfer of bacteria from 3 to 8% NaCl media was carried out both by abrupt change (shock) and by gradual change. For abrupt change, cells in the 3% NaCl medium were harvested by centrifuging at 10,000 × *g* and suspended in 8% NaCl in either artificial seawater or 8% NaCl-YP medium. Gradual change in salinity (3 to 8% NaCl) was brought about by dialyzing the cell suspension against a continuously increasing gradient of NaCl over 8 h. Survival of the cells after different periods of exposure in the high NaCl concentration was determined by plating on 3% NaCl YP agar plates and counting the colonies. In parallel, the portion of the population capable of forming colonies on 8% NaCl YP agar was estimated and expressed as percent of total on 3% NaCl.

Competition experiments between different luminous bacterial species. Experiments were carried out both in batch and in continuous culture conditions with an inoculum mixture of *B. harveyi* and *P. leiognathi* strains of equal density. The ratio between these strains was followed throughout growth. The media used were 3% NaCl-YP medium and basal medium with 0.3% glycerol (23). For the competition experiments in continuous culture conditions, a chemostat (Bioflow model C30; New Brunswick Scientific Co., Inc., New Brunswick, N.J.) with a flow rate of 0.3 ml·min^{-1}, agitated at 400 rpm, and an aeration of 0.2 (vol/vol)·min^{-1} was used. The total volume in the culture vessel was 300 ml. Plating was carried out on YP agar containing 3% NaCl and 0.2% soluble starch to differentiate between *B. harveyi* strains which are amylase positive and *P. leiognathi* strains which are amylase negative. Extracellular amylase production was detected as described in a previous paper (23).

RESULTS

Growth temperatures. Luminous bacteria strains isolated from different environments or during different seasons differed markedly in growth temperature minima and maxima and also in growth rates and cell yields for different temperatures (Fig. 1 and Table 1). All Mediterranean winter strains, *B. harveyi* as well as *P. fischeri*, grew at 10°C, but many did not grow at 40°C. On the other hand, summer *B. harveyi* isolates grew well at 40°C but did not grow at 10°C. At 15°C, growth of summer isolates was significantly lower than that of the winter strains, whereas at 34°C, the summer strains outgrew the winter ones, although the difference in rate was minimal (Table 1). Thus, the seasonal selection of thermal types of luminous bacteria in the coastal waters of the eastern Mediterranean basin seems to be due to different growth temperature spectra of the principal types of luminous bacteria.

Sensitivity to photooxidative damage. Luminous bacteria differ in sensitivity to photooxidation, as demonstrated in the laboratory

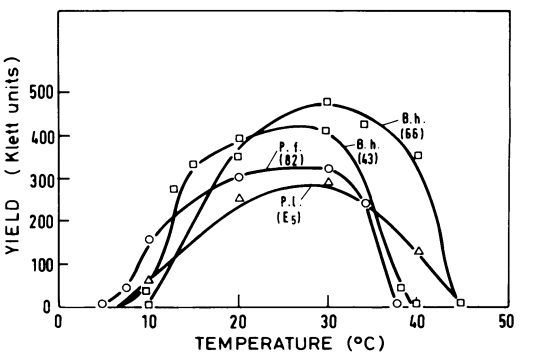

FIG. 1. *Growth yield of different strains of luminous bacteria at different temperatures in YP medium. Yield was measured after 24 h in Klett units at the stationary phase of growth; 100 Klett units (filter 420) = 0.7 × 10^8 cells per ml.*

under an atmosphere of pure oxygen (Fig. 2a) and in in situ experiments in the marine environment (Table 2). In the laboratory, typical *B. harveyi* isolates from both the Mediterranean Sea and the Gulf of Elat showed a relatively high degree of resistance, whereas all the *P. leiognathi* and *P. fischeri* strains were much more sensitive to a light intensity of 10^6 ergs·cm^{-2}·s^{-1}, approximating that of the Elat surface waters during the summer (Fig. 2a).

In laboratory experiments, addition of the toluidine blue (1 μM) sensitized different *B. harveyi* strains to a much lower light intensity (10^3 ergs·cm^{-2}·s^{-1}) (Fig. 2b). The critical importance of light intensity is demonstrated in in situ photooxidation experiments carried out at different depths. At the surface, *P. leiognathi* populations are drastically curtailed, whereas at 6 m depth, with a reduction of light intensity (50%), the photolethal effect on *P. leiognathi* was markedly reduced (Table 2). This was not observed in similar experiments with *P. fischeri*.

Densitometric scans of polyacrylamide gel electrophoresis of *B. harveyi* and *P. leiognathi* extracts were carried out for qualitative and quantitative comparison of SOD activity. Both qualitative and quantitative results showed a similar pattern of two activity bands (Fig. 3). In both organisms these peaks of SOD activity were not diminished after 60 min of illumination at 10^6 ergs·cm^{-2}·s^{-1}, an intensity which reduces the viable count of *P. leiognathi* (strain 602) by several logs without having any noticeable effect on the viability of *B. harveyi* (strain 614). Thus, the higher resistance of *B. harveyi* to photooxidative damage could not be due to its SOD activity.

Nutritional requirements. As noted above,

TABLE 1. *Temperature growth characteristics of summer and winter strains of Mediterranean B. harveyi*[a]

Growth temp (°C)	Strain	Doubling time	Yield[b]
10	W (30, 43)	8–24 h	55
	S (53)	NG	NG
15	W (43)	120 min	400
	S (53)	210 min	325
20	W (30, 43)	70 min	400
	S (42)	70 min	400
34	W (30, 43)	30 min	550
	S (23)	25 min	550
40	W (30, 43)	NG	NG
	S (23)	30 min	400

[a] Medium used was YP–3% NaCl. W, Winter; S, summer; NG, no growth.

[b] Values indicate Klett units; 100 Klett units (filter 42) = 1.0 × 10^8 cells.

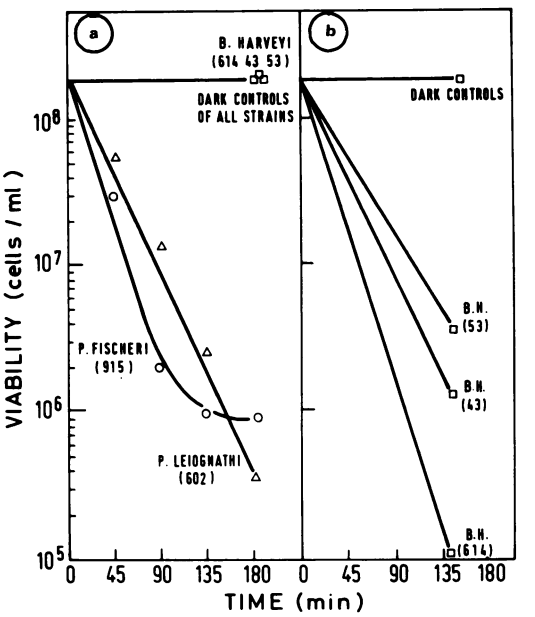

FIG. 2. *Photooxidative death of B. harveyi strains (43, Mediterranean, winter; 53, Mediterranean, summer; 614, Gulf of Elat coast, summer), of a typical P. fischeri strain (915, Mediterranean, winter), and of P. leiognathi (602, Gulf of Elat, summer). (a) Photosensitizer not added; (b) photosensitizer (toluidine blue, 1 μM) added.*

TABLE 2. *Effect of photooxidative damage on different luminous bacteria immersed in cellophane bags in the sea*[a]

Conditions	No. of cells					
	B. harveyi		*P. leiognathi*		*P. fischeri*	
	Light	Dark	Light	Dark	Light	Dark
Zero time	1.9 × 10^9		4.0 × 10^8		1.4 × 10^9	
At surface[b]	3.5 × 10^8	2.0 × 10^9	2.8 × 10^4	3.5 × 10^8	1.2 × 10^5	4.0 × 10^8
At 6 m[c]	1.0 × 10^9	2.5 × 10^9	1.5 × 10^8	3.5 × 10^8	4.0 × 10^4	4.0 × 10^8

[a] Cells harvested from overnight cultures in YP medium were centrifuged and suspended in sterile seawater.

[b] Light intensity at surface was 10^6 ergs·cm^{-2}·s^{-1}.

[c] Light intensity at 6 m depth was 5 × 10^5 ergs·cm^{-2}·s^{-1}.

during the winter and spring season, *P. leiognathi* and *B. harveyi* coexist in the coastal regions of the Gulf of Elat where the light conditions are sufficiently low for *P. leiognathi* survival. However, in the deeper parts of the Gulf of Elat, during the year round, *P. leiognathi*, present throughout the depth profile, is the only type found. It is therefore important to determine the factors enabling *B. harveyi* to multiply only in the strip between the coast and the reef, and excluding it from the open and deeper waters of the Gulf.

The assumption that nutrient requirements might explain this *B. harveyi* distribution was tested. The open waters of the Gulf are extremely poor in nutrients, whereas the coastal strip between the coral reef and the shore line where *B. harveyi* thrives has relatively high nutrient concentrations, and chlorophyll *a* content and primary production are also much greater (13, 22).

Experiments on competition between *B. harveyi* and *P. leiognathi* in batch culture conditions carried out at two different temperatures and in rich and in minimal media (0.3% glycerol) resulted in rapid domination of *P. leiognathi* by *B. harveyi* (Table 3). In continuous culture (flow rate of 0.3 ml/min), competition between an Elat strain of *B. harveyi* (strain 614) and *P. leiognathi* (strain 602) in the minimal medium (0.3% glycerol) resulted in complete domination of *B. harveyi* over the *P. leiognathi* within 9 to 10 days (at 26°C) (Fig. 4). We have not yet succeeded in obtaining growth conditions in batch or chemostat cultures for *P. leiognathi* to overgrow *B. harveyi*.

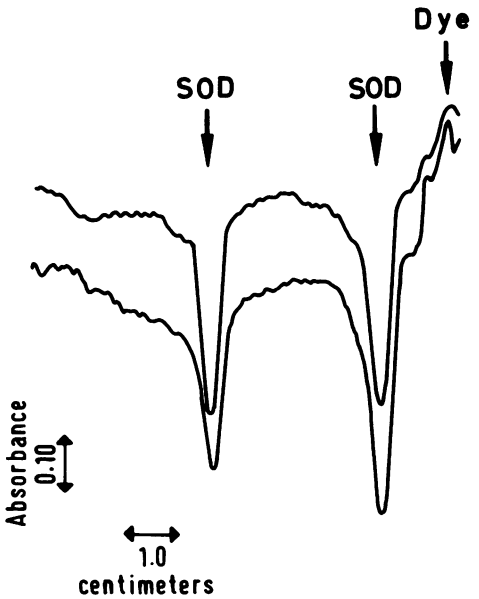

FIG. 3. *Color scan of SOD activity in polyacrylamide gel (see text). Base line of scale was shifted to separate two scans. Upper line indicates B. harveyi (strain 614); lower line indicates P. leiognathi (strain 602).*

Resistance to high salt concentration. Different luminous bacteria have a different salinity range for growth. *P. fischeri* and *P. leiognathi* did not grow on 8% NaCl-YP medium (Fig. 5), whereas the *B. harveyi* strains had a wide growth range (1 to 8% NaCl). This explains the fact that only *B. harveyi* strains are found inside the Bardawil hypersaline lagoon, whereas *P. fischeri* are found, but only rarely, at the inlets.

Survival of Mediterranean *B. harveyi* strains transferred from 3 to 8% NaCl is markedly less than strains isolated from the hypersaline Bardawil lagoon (Fig. 6). This is more pronounced where cells were shocked by direct transfer from 3 to 8% NaCl or 8% artificial seawater than where cells were subjected to a gradual change in salinity.

Transfer of *B. harveyi* cells from 3% into 8% NaCl-YP medium protected even the highly sensitive Mediterranean strains from the lethal effects of salt shock. Survival in 8% NaCl-YP medium was high (nearly 100%) even when chloramphenicol (100 μg/ml) was added to prevent growth (Fig. 7). Transfer of cells from low to high salt concentrations using artificial seawater gave results similar to transfer in NaCl alone. The capacity of cells to grow on YP medium with 8% NaCl was markedly higher for Bardawil isolates (10 to 100% of total), as compared with the coastal *B. harveyi* strains from the Mediterranean Sea (10^{-3}% of total).

DISCUSSION

Environmental factors seem to control the population dynamics of free-living luminous marine bacteria and to account both for the geo-

TABLE 3. *Competition between P. leiognathi and B. harveyi in batch conditions at different temperatures and in different media*[a]

Time (h)	*P. leiognathi* strain 602 cells per total luminescent bacteria (%)			
	YP (15°C)	YP (30°C)	MM (15°C)	MM (30°C)
0	50	50	50	50
24	14	0.2	14	0.4
48	10	0	0	0

[a] Inoculum: *P. leiognathi* (strain 602), 10^8 cells, and *B. harveyi* (strain 614), 10^8 cells. MM, Minimal medium.

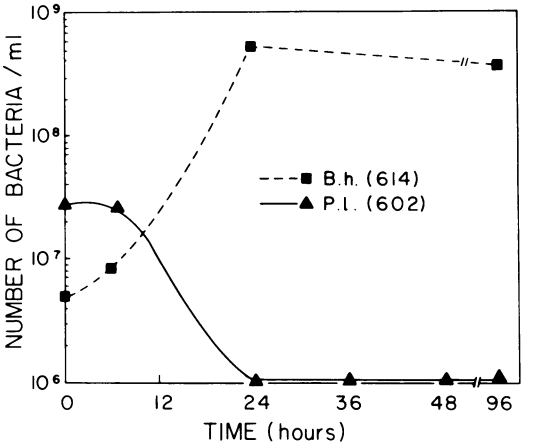

FIG. 4. *Competition between P. leiognathi (P.l.) and B. harveyi (B.h.) in a chemostat. Portions were removed at different times, and colonies were counted differentially on amylase-YP and distinguished by amylase production. Growth conditions were as described in the text.*

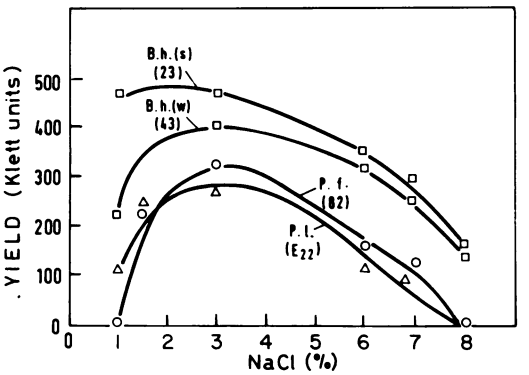

FIG. 5. *Growth yield of different strains of luminous bacteria (P. leiognathi [P.l.] and B. harveyi [B.h.]) at different concentrations of NaCl-YP medium. Yield was measured after 24 h in Klett units at the stationary phase of growth; 100 Klett units (filter 420) = -0.7×10^8 cells per ml.*

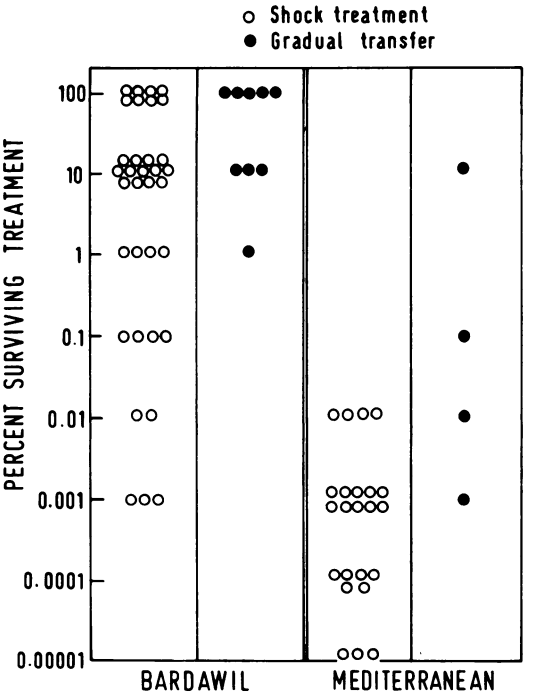

FIG. 6. *Survival after transfer from 3 to 8% NaCl solution. Strains investigated: Bardawil, no. 1, 13, 21, 504, 111B, 111C, 111F, 111E; Mediterranean, no. 30, 59, 43, 901, 903, 920, B, C, D. Each point represents a different isolate.*

graphic distribution of the different types and for their seasonal fluctuations. Our results indicate that the distribution pattern in the eastern Mediterranean and the Gulf of Elat is presumably affected by at least four major factors (not all of which may be critical at a given location): water temperature, light intensity, nutrient concentration, and salinity. The adaptability of the different types to these parameters governs their distribution. In the Mediterranean Sea, seasonal temperature fluctuations seem to select for thermal and taxonomic types of bacteria, with both winter minimum and summer maximum temperatures having a direct effect on alternations of different *B. harveyi* populations and on the disappearance of *P. fischeri* in summer. However, even before the temperature peaks are reached, differences in relative growth rates may explain the enrichment in winter or summer types with changing temperature conditions. Thus, at 34°C, growth of *B. harveyi* summer types slightly exceeds that of winter types (Table 1), whereas at 15°C, growth of the winter types significantly exceeds that of the summer types (Table 1).

The seasonal fluctuation observed in the Mediterranean Sea (23; Shelubsky-Shilo, M. S. thesis, 1943), in the North Sea (5), and in the Pacific Ocean (20) contrasts with the continuity and relative constancy in numbers and species composition in the main water body of the Gulf of Elat. This constancy is mainly due to the stability of the temperature (21 to 26°C) throughout the entire water profile and throughout the year. Lower water temperatures seem to be the decisive factor in the permanent presence of the cold-water forms of *P. phosphoreum* in the North Sea (5), and of *P. fischeri* in the California coast (temperatures below 23°C [20]). In both these bodies of water, *B. harveyi* only occurs as

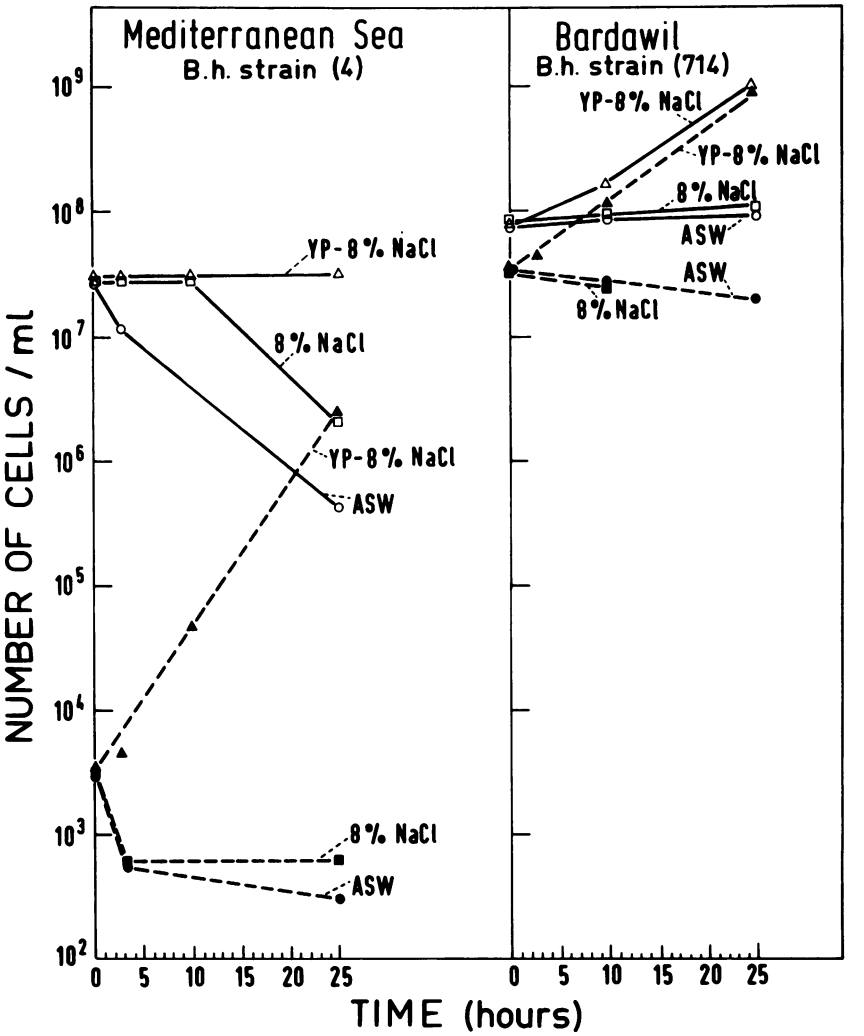

FIG. 7. *Survival and capability of growth of typical B. harveyi (B.h.) Mediterranean (4) and Bardawil (714) strains in 8% NaCl-YP medium after sudden transfer from 3 to 8% NaCl in different media. Solid line and open symbols indicate viability tested by capability of forming colonies on 3% YP medium. Broken line and closed symbols indicate capability for growth on 8% NaCl-YP medium. Treatment media: △, YP-8% NaCl; □, 8% NaCl; ○, 8% artificial seawater (ASW).*

a summer intrusion. Already in 1916, Beijerinck observed that the growth temperature optimum of *B. harveyi* in laboratory media was much higher than that of *P. phosphoreum* and that this could explain the distribution of these species. In the eastern Mediterranean, with an annual oscillation between 15 and 30°C, *P. fischeri* is found only during the winter and the spring. In the Gulf of Elat, where temperatures never fall below 20°C, *P. fischeri* is never found.

The selection of different symbiotic luminous bacteria inhabiting the light organ of different fishes also appears to be governed by the water temperatures. Thus, some of the cold-water deepsea fishes, including representatives belonging to several families of different orders, are inhabited by *P. phosphoreum* (20). This group of luminous bacteria is characterized by its capacity to grow at 4°C and also seems to survive high pressure better than either *P. fischeri* or *B. harveyi* (6). *Leiognathidae*, which are typical tropical shallow-water Pacific fishes living in temperatures from 25 to 30°C, have light organs inhabited by the warm-water bacterium, *P. leiognathi* (17). *Monocentridae*, subtropical and temperate relatively shallow-water fishes, are found in Australian, Japanese, South African, and South American coastal waters, where tem-

peratures range from 15 to 20°C. The symbiotic luminous bacterium inhabiting their light organs is the mesotropic species, *P. fischeri* (10, 19).

In the Gulf of Elat, *P. leiognathi*, the sole free-living luminous bacterium of the open water, is present in the entire column below 2 m depth; its absence from shallow coastal areas and the surface layer of open water in summer can now be explained as due to solar radiation-induced decay. Only the more photoresistant *B. harveyi* can survive under the strong light conditions prevailing in the shallow coastal region during the summer. In in situ experiments, a single day of exposure to sunlight of a mixed *P. leiognathi* and *B. harveyi* culture submerged in cellophane tubes reduced the viable count of *P. leiognathi* by several orders of magnitude, whereas the *B. harveyi* population was hardly affected.

Differences in sensitivity to photodynamic effects are widely known from different organisms; however, this may be the first description of lethal photooxidation governing composition of indigenous bacterial communities in oceans. Differences in resistance to photooxidation may explain the distribution of luminous bacteria on the Hawaiian coast, where *P. leiognathi*, *P. phosphoreum*, and *B. harveyi* were present in approximately equal numbers in the open waters off Oahu, whereas *B. harveyi* was the sole or predominant species in the coastal waters (16).

A photooxidative decay model has likewise been presented for enteric bacteria in seawater by Chamberlin and Mitchell (7) in their analysis of the field data of Gameson and Gould (11) where indications were found that there is a linear relationship between decay rates and light intensity. Thus, light was proposed as the major factor controlling mortality of enteric bacteria in marine environments. This does not exclude the possibility that additional factors can accentuate or may even be essential to photooxidative damage.

The intensity of light was found to be critical; the slight decrease in light intensity at several meters depth below the surface was sufficient to markedly reduce the photolethal effect on *P. leiognathi* (Table 2). The addition of toluidine blue photosensitizer destroyed the natural resistance of *B. harveyi* to photooxidation, and it became as sensitive to light and oxygen as *P. leiognathi* and *P. fischeri* (Fig. 5). This suggests that the high sensitivity of *P. leiognathi* and *P. fischeri* to light may be due to the presence of a natural photosensitizer such as the phorphyrin pigments.

Nutrient concentration may also control the distribution of some species. *B. harveyi* thrives in such eutrophic marine enviroments as the Mediterranean shore, enriched by local sewage outfalls, by flood waters from agricultural land, by winter mixing, and by upwelling during summer (O. Oren, Ph.D. thesis, Hebrew University of Jerusalem, 1970). In the Gulf of Elat, *B. harveyi* was present only in the coastal strip between the coral reef and the shore, a region markedly higher in nutrient concentration, primary production and chlorophyll *a* content than the open water region (13, 22). The Gulf of Elat, which is surrounded by desert, is characterized by low nutrient concentrations throughout the entire water column. We suggest that the oligotrophic conditions prevailing in the Gulf favor the selective enrichment of *P. leiognathi* over *B. harveyi*. Competition experiments between Gulf of Elat *B. harveyi* and *P. leiognathi* strains in batch culture as well as in the chemostat confirmed the superiority of *B. harveyi* over *P. leiognathi* when rich or less rich minimal media were used (Fig. 4, Table 3). We suggest that our inability to obtain conditions for selective enrichment of *P. leiognathi* is due to the fact that even the minimal medium is "rich" when compared with the nutrient concentrations of Gulf of Elat water. We predict that this oligotrophic species has a lower threshold level for nutrient concentrations than *B. harveyi* does.

The effect of salinity has been investigated in populations from the Bardawil lagoon, a hypersaline body of water surrounded by the Mediterranean Sea and separated from it by a narrow bar but with a constant inflow of Mediterranean water taking place. For survival and growth in the lagoon, tolerance to high salt concentrations (8%) is required. Most *B. harveyi* types and all *P. fischeri* types appear to be eliminated in the lagoon owing to their sensitivity to salt shock. Only halo-tolerant types or mutants of *B. harveyi* are capable of surviving and multiplying in this environment. This inference is supported by the distribution of luminous bacteria along a transect extending from the opening of the lagoon toward its inner, most saline part, sampled in August 1978. The percentage of cells capable of colony formation on 8% YP agar showed a marked increase from the Mediterranean inlets toward the hypersaline part of the lagoon, indicating that selection or enrichment for saline-tolerant types had taken place. An interesting case of differences in sensitivity to cation shock among yeast strains and their mutants has been described by Bard et al. (2) where differences in the membrane sterol composition between the wild type and its mutants seemed to underlie the sensitivity to lethal cation pulses in the yeast.

In conclusion, the notion that luminous bacteria can serve as valuable tools in indicating the presence of different water masses is supported. Moreover, information has been obtained on the physiological factors which govern and control distribution of luminous bacteria, and these findings may now be extended to other bacterial groups.

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LITERATURE CITED

1. **Abeliovich, A., and M. Shilo.** 1972. Photooxidative death in blue-green algae. J. Bacteriol. **111**:682-689.
2. **Bard, M., N. D. Lees, K. S. Burrows, and F. W. Kleinhans.** 1978. Difference in crystal violet uptake and cation-induced death among yeast sterol mutants. J. Bacteriol. **135**:1146-1148.
3. **Beauchamp, C. O., and I. Fridovich.** 1971. Superoxide dismutase: improved assays and an assay applicable to polyacrylamide gels. Anal. Biochem. **44**:276-287.
4. **Beijerinck, M. W.** 1889. Le *Photobacterium luminosum*, bacterie luminesce de la Mer du Nord. Arch. Neerl. Sci. Exacta Nat. Haarlem. **23**:401-405.
5. **Beijerinck, M. W.** 1916. Leuchtbakterien der Nordsee in August und September. Folia Microbiol. (Delft) **4**:15-40.
6. **Brown, D. E., F. H. Johnson, and D. A. Marsland.** 1942. The pressure temperature relations of bacterial luminescence. J. Cell. Comp. Physiol. **20**:151-168.
7. **Chamberlin, C. E., and R. M. Mitchell.** 1978. A decay model for enteric bacteria in natural waters, p. 325. *In* R. Mitchell (ed.), Water pollution microbiology. Wiley-Interscience, New York.
8. **Davis, B. J.** 1964. Disc electrophoresis. 2. Method and application to human serum proteins. Ann. N.Y. Acad. Sci. **121**:404-427.
9. **Eloff, J. N., Y. Steinitz, and M. Shilo.** 1976. Photooxidation of cyanobacteria in natural conditions. Appl. Environ. Microbiol. **31**:119-126.
10. **Fitzgerald, J. M.** 1977. Classification of luminous bacteria from the light organ of the Australian pinecone fish, *Cleidopus gloriamaris*. Arch. Microbiol. **112**:153-156.
11. **Gameson, A. L. H., and D. J. Gould.** 1975. Proceedings of the International Symposium on Discharge of Sewage from Sea Outfalls. Pergamon Press, Inc., Elmsford, N.Y.
12. **Krinsky, N. I.** 1968. The protective functions of carotenoid pigments. Photophysics **3**:123-195.
13. **Levanon-Spanier, I., E. Padan, and Z. Reiss.** 1979. Primary production in a desert-enclosed sea—the Gulf of Elat (Aqaba), Red Sea. Deep Sea Res., in press.
14. **Lowry, O. H., N. J. Rosebrough, A. L. Farr, and R. J. Randall.** 1951. Protein measurement with the Folin phenol reagent. J. Biol. Chem. **193**:265-275.
15. **McCord, J. J., and I. Fridovich.** 1969. Superoxide dismutase—an enzymic function for erythrocuperin (Hemocuperin). J. Biol. Chem. **244**:6049-6055.
16. **Reichelt, J. L., and P. Baumann.** 1973. Taxonomy of the marine, luminous bacteria. Arch. Mikrobiol. **94**: 283-330.
17. **Reichelt, J. L., K. Nealson, and J. W. Hastings.** 1977. The specificity of symbiosis: pony fish and luminescent bacteria. Arch. Microbiol. **112**:157-161.
18. **Ruby, E. G., and K. H. Nealson.** 1976. Symbiotic association of *Photobacterium fischeri* with the marine luminous fish *Monocentris japonica*: a model of symbiosis based on bacterial studies. Biol. Bull. (Woods Hole, Mass.) **151**:574-586.
19. **Ruby, E. G., and J. G. Morin.** 1978. Specificity of symbiosis between deep-sea fishes and psychrotrophic luminous bacteria. Deep Sea Res. **25**:161-167.
20. **Ruby, E. G., and K. Nealson.** 1978. Seasonal changes in the species composition of luminous bacteria in nearshore seawater. Limnol. Oceanogr. **23**:530-533.
21. **Spikes, J. D., and R. Livingston.** 1969. The molecular biology of photodynamic action sensitized oxidations in biological systems. Adv. Rad. Biol. **3**:29-121.
22. **Sournia, A.** 1977. Notes on primary productivity of coastal waters in the Gulf of Elt (Red Sea). Int. Rev. Ges. Hydrobiol. **62**:813-819.
23. **Yetinson, T., and M. Shilo.** 1979. Seasonal and geographic distribution of luminous bacteria in the Eastern Mediterranean Sea and the Gulf of Elat. Appl. Environ. Microbiol. **37**:1230-1238.