APPLIED AND ENVIRONMENTAL MICROBIOLOGY, Jan. 1991, p. 295–300
0099-2240/91/010295-06$02.00/0

Vol. 57, No. 1

Distribution and Physiology of Aerobic Bacteria Containing Bacteriochlorophyll *a* on the East and West Coasts of Australia†

TSUNEO SHIBA,[1] YUZO SHIOI,[2] KEN-ICHIRO TAKAMIYA,[3]* DAVID C. SUTTON,[4] AND CLIVE R. WILKINSON[5]

Otsuchi Marine Research Center, Ocean Research Institute, University of Tokyo, Iwate,[1] Division of Biology, Miyazaki Medical College, Miyazaki,[2] and Department of Biology, Faculty of Science, Kyushu University, Fukuoka 812,[3] Japan, and Sir George Fisher Center for Tropical Marine Studies, James Cook University of North Queensland,[4] and Australian Institute of Marine Science,[5] Townsville, Australia

Received 11 July 1990/Accepted 31 October 1990

Aerobic heterotrophic bacteria containing bacteriochlorophyll were isolated from specimens from a wide variety of marine environments on the west (Shark Bay, Lake Clifton, Lake Heyward, and Perth) and east (near Townsville and Brisbane) coasts of Australia. The bacteria were found in a high proportion (10 to 30%) of the total heterotrophic bacterial strains isolated from marine algae, seagrasses, stromatolites, the epiphytes on stromatolites, seawater, and sands; in some cases they constituted up to 49% of the total. This is much higher than the previous report of 6% from Japan. A high percentage, 13%, was also found in the seawater of Hamelin Pool, at Shark Bay, where the salinity was 66‰. The number of these bacteria was generally low in seawater and sands, with a few exceptions. There were no aerobic bacteriochlorophyll-containing bacteria on sponges or corals. The isolated strains were orange or pink, and most had absorption maxima around 800 and 850 to 870 nm, the latter range being the absorption of bacteriochlorophyll *a* in vivo. The maximum bacteriochlorophyll content was 1 nmol/mg (dry weight) of bacterial cells. Most of the bacteria did not grow phototrophically under anaerobic conditions in a broth medium containing succinate. Cells and cell extracts grown under aerobic conditions had photochemical activities such as reversible photooxidations of the reaction center and cytochrome(s). Some strains showed denitrifying activity. The optimal salinity for bacterial growth varied between strains.

Aerobic heterotrophic bacteria containing bacteriochlorophyll (Bchl) (i.e., aerobic Bchl-containing bacteria [ABB]) have been isolated from a wide variety of marine environments in Japan (18). These bacteria can grow heterotrophically under aerobic conditions in the dark. They are different from the known nonsulfur purple bacteria in that they are unable to grow phototrophically under anaerobic conditions (17), despite the possession of a photosynthetic apparatus (6). This apparatus operates under aerobic conditions but not under anaerobic conditions, and therefore these bacteria have been called aerobic photosynthetic bacteria (1, 7, 10, 13, 16, 22). Some strains can grow by using anaerobic respiratory or denitrification systems in the presence of auxiliary oxidants such as trimethylamine *N*-oxide (1) or nitrate (20). The ecological and evolutionary significance of the presence of Bchl and the photosynthetic system is not clear, since these bacteria have been found to be only a small proportion (average, about 1%; maximum, 6%) of the total heterotrophic community in some areas of Japan (18). Some investigators have suggested that ABB are phototrophic bacteria which have adapted to aerobic environments and that they lose Bchl during the adaptation process (1, 12). The number of ABB in Japan was too low to study the wide distribution and to show the general pattern of low-Bchl content in ABB.

In this paper, we describe the distribution of ABB in the sea and saline lakes of the west and east coasts of Australia.

MATERIALS AND METHODS

Sampling. The specimens examined were marine algae, seagrasses, stromatolites, the epiphytes on the stromatolites, sponges, corals, sands, and seawater. They were collected from the intertidal flats of Shark Bay (which is very shallow and has a very low diversity of fauna at high salinity [11]), at Lake Clifton and Lake Heyward (both of which are isolated saline lakes), at a rocky beach near Perth, from intertidal flats of Magnetic Island (Arcadia Bay), at the rocky beaches (Horseshoe and Radical Bay) of Magnetic Island, at the intertidal flats near Brisbane, at a mud flat near Cape Cleveland (which was about 1 m in depth at low tide), and from the coral environment of Orpheus Island (Fig. 1). On the west coast, water temperatures were 20 to 23°C and salinity was 18 to 66‰ (Table 1). On the east coast, water temperatures were 28 to 32°C near Townsville and 21°C near Brisbane, and salinity was 32 to 34‰. The specimens were washed and then homogenized in sterilized seawater either with a glass homogenizer or blender. After serial decimal dilution of the homogenates in sterilized seawater, 0.1 ml of each dilution was spread on PPES-II agar plate medium (21). A modified PPES-II medium with double-strength seawater was also used to isolate bacteria from high-salinity environments (Table 1). Plates were incubated at 25°C in the dark, and CFU were counted after 10 days. Pigmented colonies were isolated and replated until pure colonies were obtained. The pure pigmented colonies were transferred to PPES-II slant agar culture medium.

Presence of Bchl in heterotrophs. After 7 to 10 days of incubation, 1 ml of acetone-methanol (7:2, vol/vol) was added to the PPES-II slant agar culture. The resulting extracts were centrifuged (1,500 × *g*, 10 min), and absorption spectra of the supernatant solutions were measured.

* Corresponding author.

† Contribution no. 524 from Australian Institute of Marine Science.

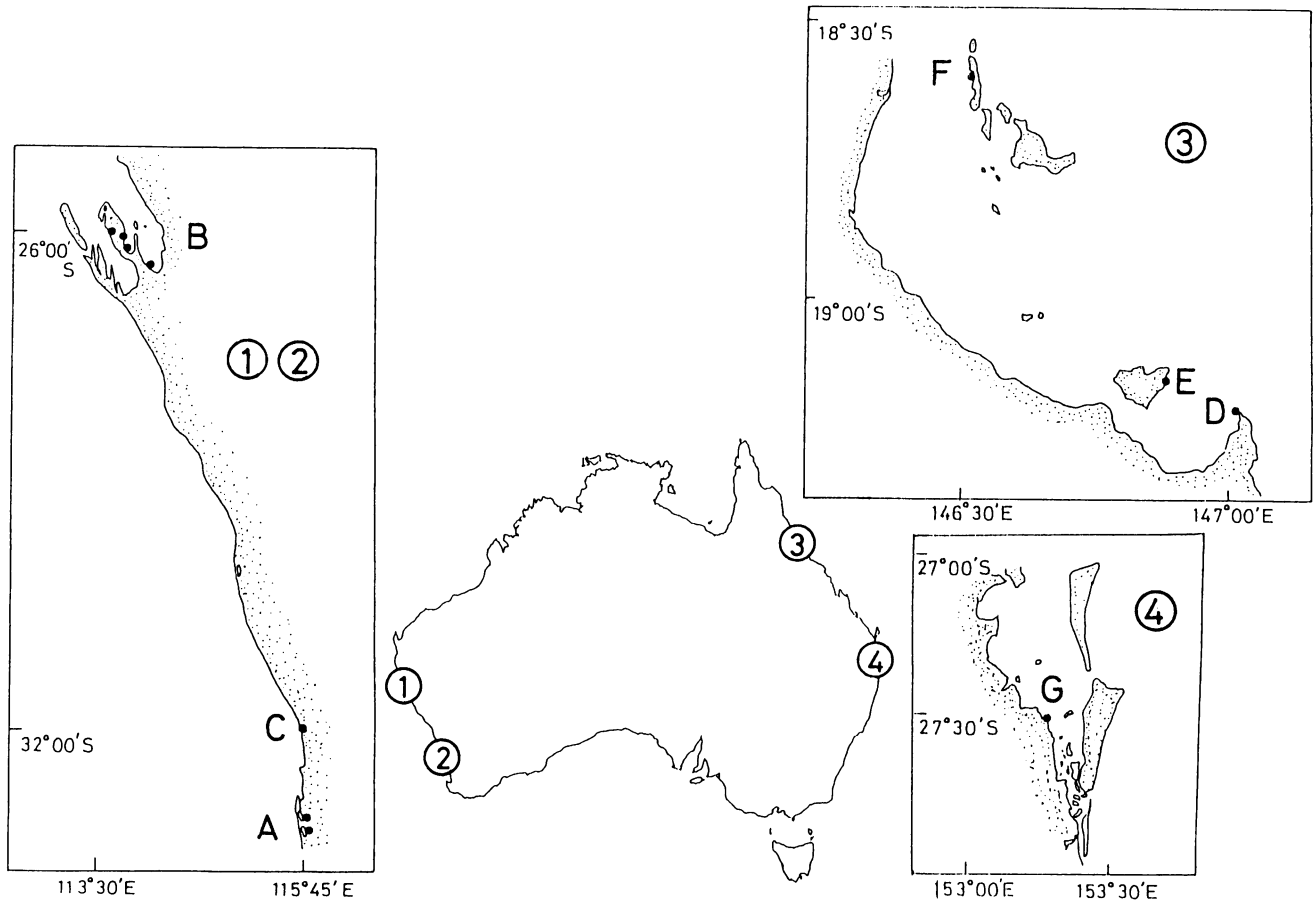

FIG. 1. Locations of sampling sites of bacteria in Australia: 1, Shark Bay; 2, Lake Clifton, Lake Heyward, and Perth; 3, Cape Cleveland, Magnetic Island, and Orpheus Island; 4, Brisbane. Figures enclosed with frames are detailed maps of sampling sites. Specific sampling sites: A, Lake Clifton and Lake Heyward; B, Shark Bay; C, Perth; D, Cape Cleveland; E, Magnetic Island; F, Orpheus Island; G, Brisbane.

The presence of Bchl *a* was confirmed by the characteristic appearance of the absorption band near 770 nm (3). Bchl content was determined with PPES-II liquid culture medium (15 ml). After collecting cells by centrifugation (5,000 × *g*, 15 min), Bchl was extracted with the mixture of acetone-methanol (7:2) as described above. Bchl content (nanomoles of Bchl per milligram [dry weight] of the bacterial cells) was determined by measuring the A_{770}. The dry weight of bacterial cells was calculated from the absorbance of the liquid culture at 660 nm. An A_{660} of 1.0 corresponded to 0.5 mg (dry weight) of bacterial cells per 1 ml of culture. The factor, 0.5, was the average of several isolated strains.

Absorption spectra of the cell suspension and cell extracts. Bacterial cells in early-stationary-phase cultures were centrifuged (5,000 × *g*, 15 min) and suspended in 40% sucrose solution. In some cases, cells were disrupted by use of a French pressure cell, and cell extracts were obtained by centrifugation at 10,000 × *g* for 30 min (supernatant solution). The absorption spectra of these samples were measured by using a Cary model 17D or Shimadzu UV240 spectrophotometer. Light-minus-dark difference spectra of cell extracts were measured with the Shimadzu UV240 spectrophotometer with a combination of optical filters. Flash-light-induced oxidation of cytochromes was measured as described previously (23).

Anaerobic growth. Anaerobic growth was examined in PPES-II broth culture supplemented with 10 mM succinate. The broth culture was covered with sterilized liquid paraffin and incubated in the light. Some strains were also examined by using a BBL GasPak anaerobic system (BBL Microbiology Systems, Cockeysville, Md.).

RESULTS AND DISCUSSION

Distribution and proportion of ABB. Numerous ABB were isolated from specimens from a wide variety of marine environments on the west and east coasts of Australia (Tables 1 and 2; Fig. 1). The percentages of ABB cultivated at two different salinities (25 and 70‰) are shown in Table 1.

There were consistently more ABB isolated from the west coast of Australia than from the east. Almost all specimens contained some ABB, with the proportion of ABB among the total number of heterotrophically cultivated strains often being between 12 and 30% (Table 1). The highest numbers of ABB were from the sands of Hamelin Pool, an unidentified seagrass at Shell Beach, *Cymodocea* sp. and *Laurencia* sp. at Little Lagoon, and *Botryocladia* sp. at Denham. The number of ABB was also high in the stromatolites of Hamelin Pool and Lake Clifton, even though the two stations had very different salinities (Table 1). Stromatolites are lithified structures formed through the binding of sediments to certain cyanobacteria and/or some algae (2, 4, 5, 8, 9, 11).

TABLE 1. Distribution of ABB in Lake Clifton, Perth, and Shark Bay, Western Australia[a]

Sample	Salinity (‰)	CFU[b]	ABB (%) at culture salinity of:	
			25‰	70‰
Lake Clifton (32°40′S)				
Water	18	3.1×10^3	4.4	—[c]
Stromatolite		10^6–10^7	6.8	—
Charophyte		10^6–10^7	5.9	—
Epiphyte of stromatolite		10^6–10^7	23.8	—
Lake Heyward (32°41′S), water	63	6.7×10^4	0.4	0.2
Shark Bay				
Monkey Mia (25°52′S)				
Water	37	9.0×10^2	1.1	—
Seaweed				
Enteromorpha linza		10^6–10^7	3.0	—
Sands		10^5–10^6	1.9	—
Denham (25°53′S)				
Water	46	7.0×10^2	0.0	0.0
Seaweeds				
Botryocladia sp.		10^5–10^6	8.1	31.8
Penicillus sp.		10^5–10^6	1.1	0.0
Sands		10^5–10^6	3.5	6.8
Little Lagoon (25°53′S)				
Water	51	1.8×10^2	0.0	0.0
Seaweeds				
Botryocladia sp.		10^5–10^6	6.8	—
Cymodocea sp.		10^4–10^5	12.1	23.2
Laurencia sp.		10^5–10^6	4.4	20.5
Shell Beach (26°10′S)				
Water	60	2.3×10^2	0.0	0.0
Seagrass[d]		10^5–10^6	17.8	23.9
Hamelin Pool (26°24′S)				
Water	66	4.4×10^2	14.9	13.4
Stromatolite		10^5–10^6	12.7	22.2
Sands		10^5–10^6	31.9	29.5
Perth (32°00′S)				
Seaweeds				
Enteromorpha sp.		10^6–10^7	5.6	—
Ulva sp.		10^5–10^6	5.5	—

[a] For locations, see Fig. 1.
[b] CFU per gram (fresh weight) using the media with 25‰ salinity.
[c] —, Not tested.
[d] Not identified.

TABLE 2. Distribution of ABB near Townsville and Brisbane[a]

Sample	CFU	ABB (%)
Cape Cleveland (19°09′S)		
Water	1.0×10^4	0.0
Seaweeds		
Caulerpa sp. 1	1.1×10^3	0.0
Caulerpa sp. 2	5.4×10^5	0.0
Seagrasses		
Cymodocea serrulata	3.6×10^5	0.0
Halimeda sp.	6.2×10^5	0.0
Halophila spinulosa	5.3×10^5	4.0
Halophila ovalis	6.6×10^5	0.0
Halodule uninervis	4.5×10^5	0.0
Sponges		
Phyllospongia lamellosa	1.6×10^7	0.0
Pseudaxinyssa sp.	1.3×10^7	0.0
Magnetic Island (19°07′S)		
Water		
Arcadia Bay	5.0×10^4	0.0
Horseshoe Bay	3.2×10^4	0.0
Radical Bay	5.2×10^3	0.0
Sands		
Arcadia Bay	2.3×10^7	0.0
Horseshoe Bay	1.2×10^5	0.0
Radical Bay	6.0×10^5	0.0
Seaweed		
Halodule wrightii	2.4×10^7	1.0
Algal mat[b]	5.6×10^6	6.7
Algal mat[b]	3.9×10^7	20.0
Orpheus Island (18°41′S)		
Water	2.8×10^2	0.0
Sands	10^6–10^7	0.0
Black patch[c]	10^6–10^7	48.8
Epiphytic green algae	10^5–10^6	1.5
Seaweeds		
Chlorodesmis sp.	10^3–10^4	0.0
Cladophora sp.	10^5–10^6	0.0
Corals		
Acropora microphthalma	10^4–10^5	0.0
Millepora tenella	10^4–10^5	0.0
Pachyseris speciosa	10^3–10^4	0.0
Pavona cactus	10^2–10^3	0.0
Sarcophyton sp.	10^5–10^6	0.0
Sinularia flexibilis	10^5–10^6	0.0
Brisbane (27°30′S)		
Water	4.0×10^3	0.0
Sands	3.0×10^6	0.0
Seaweeds		
Acanthophora sp.	6.1×10^6	2.4
Brongoniartella sp.	1.4×10^6	0.0
Cladophoropsis magma	2.5×10^6	0.5
Codium sp.	2.2×10^7	0.7
Dictyota sp.	8.9×10^6	2.1
Laurencia concreta	7.4×10^6	7.8
Laurencia venusta	5.0×10^7	0.9
Polysiphonia sp.	1.9×10^5	0.0
Seagrasses		
Cymodocea sp.	1.2×10^6	0.4
Halophila ovalis	3.8×10^7	2.3
Halophila ovata	3.9×10^7	4.0
Halophila spinulosa	8.9×10^6	0.5

[a] For locations, see Fig. 1.
[b] Not identified.
[c] Probably cyanobacterial.

In contrast, many of the specimens from the east coast had very few or no ABB among the heterotrophic bacteria (Table 2). The specimens were collected from sites apparently similar to those on the west coast, e.g., algal and sand specimens from intertidal flats near Brisbane and Magnetic Island, but the majority of specimens had no ABB. At Cape Cleveland, ABB were isolated from only one specimen, although many algae and seagrasses were analyzed. No ABB were isolated from sponges or corals, although the presence of cyanobacteria in sponges has been reported (24).

The numbers of ABB from many Australian locations (e.g., Shark Bay and Lake Clifton) were much higher than those reported previously (about 1%) from marine environments in Japan (18). The reasons for these marked differences are unknown, but we suggest several possible explanations for these variations which relate either to the nature of the specimens or to the nature of the habitats where these specimens occur or both. Large numbers of ABB were found on stromatolites which occur only in several isolated habitats (Shark Bay [2, 9, 11] and Lake Clifton [8] in Western Australia and Exuma Islands in the Bahamas [4, 5]). These habitats feature either elevated salinities, strong sunlight and

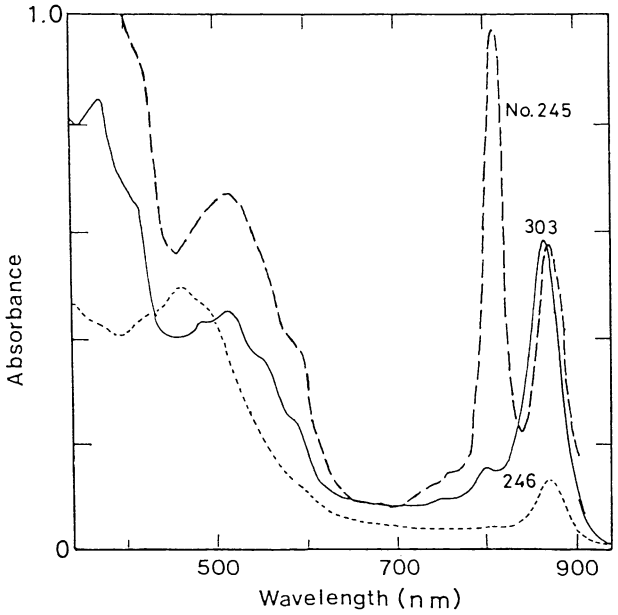

FIG. 2. Absorption spectra of cell extracts of three strains of ABB isolated in Australia: no. 245, Lake Clifton; no. 246, Lake Clifton; no. 303, Perth.

aerial exposure, or strong currents and absence of algal grazing predators (5). It is possible that the environment of a stromatolite features extremes of oxygen concentration, from supersaturation during the day to near anaerobiosis at night (2, 9).

Some algal mats also had high numbers of ABB. These mats experience similar extremes of environmental conditions, with wide variations in oxygen tension and degrees of wetting. The environmental extremes of oxygen, sunlight, and desiccation may be selective agents either for ABB or against other heterotrophic bacteria, so that the apparent proportion of ABB will increase. Few ABB were isolated from seawater or subtidal sands which would generally not experience wide fluctuations in either temperature, oxygen tension, or desiccation.

We do not have sufficient data, however, on the ecophysiology of these bacteria or their habitats to provide more definitive reasons for the apparent marked differences between Australian and Japanese habitats. Finally, we cannot exclude the possibility that Japanese water may have more specific growth requirements than those in Western Australia and PPES-II medium may be more suitable for ABB in Australia than for those in Japan.

Absorption spectra of ABB. We isolated about 300 pure strains of ABB in the present study. All of the ABB were pink or orange pigmented. Figure 2 shows the absorption spectra of cell extracts of three representative strains. Absorption bands in the near-infrared region were due to Bchl bound to proteins in vivo; those around 500 nm were due to carotenoids. The location and height of each peak varied between strains. Orange-pigmented cells usually had lower absorption bands of Bchl in the near-infrared region than those of carotenoids, and in the pink-pigmented cells the heights of the bands in both regions were similar. These absorption spectra were very similar to those of *Erythrobacter longus*, *Roseobacter denitrificans*, and *Erythrobacter* sp. OCh 175 (6, 15). (Recently *Erythrobacter* sp. OCh 114 was

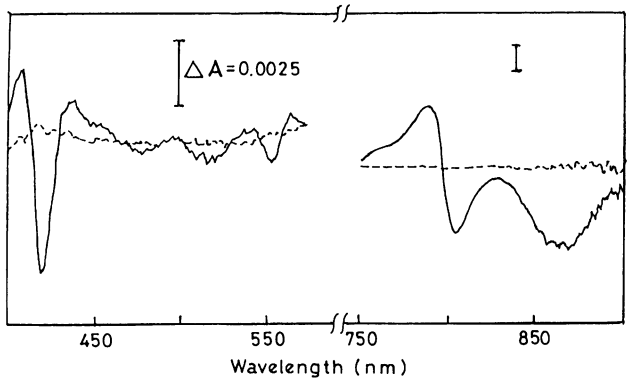

FIG. 3. Light-minus-dark difference spectra of cell extracts of strain 303. In the infrared region, oxidation of the reaction center is shown; in the visible region, oxidation of cytochrome(s) is shown. Dashed lines represent baselines.

renamed *Roseobacter denitrificans* [14].) The absorption spectra of acetone-methanol extracts from all of the strains isolated had an absorption maximum at 770 nm (data not shown), indicating that the bacteriochlorophyll was Bchl *a*. We have not yet determined whether phytol is the esterifying alcohol of Bchl *a*.

Photochemical activities of ABB. The cellular Bchl level of most strains examined was less than 1 nmol/mg (dry weight) of bacterial cells. Although this was very low compared with that of nonsulfur purple bacteria (usually 20 to 30 nmol/mg [dry weight] of bacterial cells), photochemical activities such as the reversible oxidations of the reaction center and of the cytochrome(s) upon illumination of photosynthetic light were observed (Fig. 3). In addition, these reactions took place only under aerobic conditions, not under anaerobic conditions (Fig. 4). A cell suspension in a cuvette layered with liquid paraffin became anaerobic as a result of respiration of bacterial cells (Fig. 4B), and oxidation of cytochrome(s) by flash light was abolished because the charge separation by flash in the photosynthetic reaction center was inhibited by overreduction of the photosynthetic electron transfer system under anaerobic conditions (1, 10, 22). The oxidation of cytochrome by flash light was observed after the introduction of air. These photochemical activities were found in all strains tested (20 strains). Similar results were obtained in the aerobic photosynthetic bacteria isolated in Japan (1, 10, 22). Most of the specimens from Australia were collected on high tidal flats which are usually exposed to strong sunshine. Thus, it appears that ABB from Australia can photoheterotrophically use sunlight as an energy source in addition to energy obtained by aerobic respiration. However, the ecological significance of the ability to use light energy in natural habitats remains uncertain. Because of the extremely low content of Bchl, ABB may not use solar energy as the major energy source, although they possess photochemical activities.

Other physiological properties. The ability to grow anaerobically in the light and the absorption spectra of cell cultures were examined for the strains isolated from Lake Clifton and Hamelin Pool. Although only one strain isolated from Lake Clifton showed light-dependent growth under microaerophilic conditions, all other strains did not grow anaerobically.

ABB were isolated from environments with a wide range of salinities (18 to 66‰). The growth in culture media with

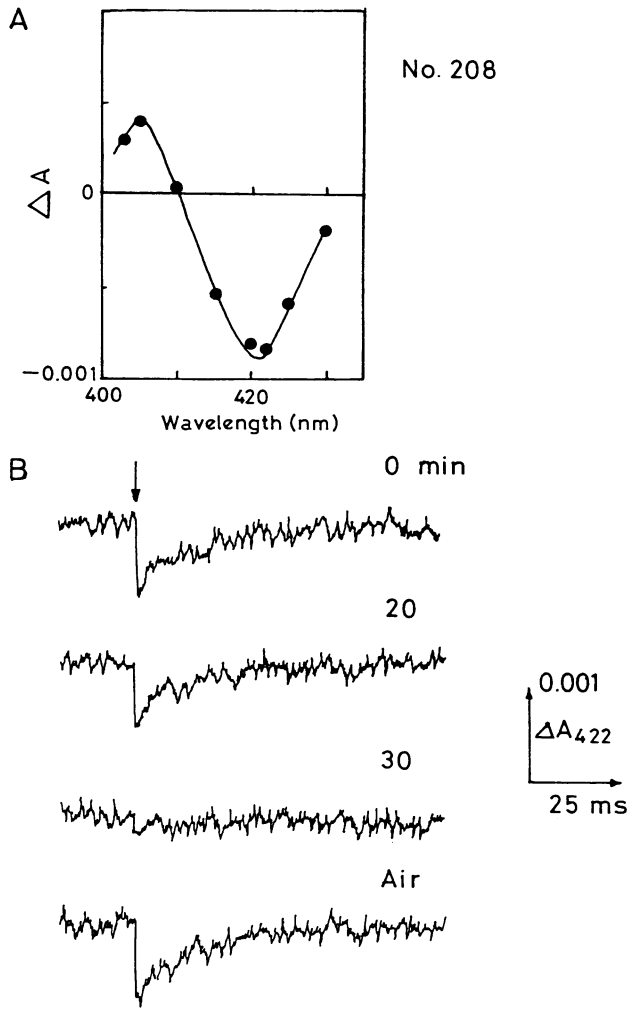

FIG. 4. Flash-light-minus-dark difference spectrum of cytochrome of whole cells under aerobic conditions in the Soret region (A) and time courses of oxidation-reduction reactions of cytochrome (whole cells) induced by flash activation under aerobic and anaerobic conditions (B). Suspension of whole cells was initially shaken in the cuvette (0 min), and liquid paraffin was layered on the suspension. The suspension became anaerobic by respiration of the cells (20 or 30 min later). Time course labeled "air" indicates that air was reintroduced into the cuvette. Arrows indicate the time when the flash light was fired. Downward displacement of trace corresponds to the oxidation of cytochrome. The strain used was 208 (Lake Clifton).

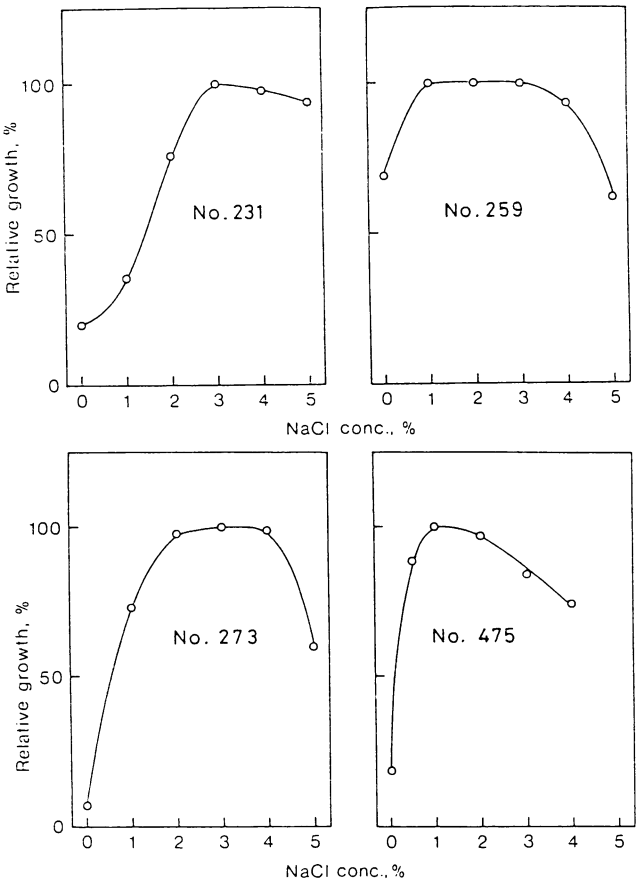

FIG. 5. Effect of salinity on bacterial growth. The optimal NaCl concentration for growth of bacteria was determined after fixing the concentrations of basal salts. The bacterial growth was measured spectrophotometrically at 660 nm after 24 h of cultivation and expressed as relative percentage. The bacteria were grown aerobically in the dark at 28°C for 24 h. The strains used were as follows: no. 231, Lake Heyward (salinity, 63‰); no. 259, Hamelin Pool (66‰); no. 273, Shell Beach (60‰); and no. 475, Brisbane (34‰).

different salinities varied according to the salinity of the habitat of the ABB (Table 1 and Fig. 5). Growth dependence on salinity has been reported in *R. denitrificans* isolated in Japan (19).

Some strains exhibited denitrifying activity (data not shown), indicating that these strains have versatile energy-transducing systems such as aerobic and anaerobic respiration, photosynthesis, and denitrification. It may be that this versatility enables them to survive under fluctuating environmental conditions. Some strains isolated from Japanese waters can grow anaerobically with nitrate or trimethylamine *N*-oxide as the electron acceptor (1, 20). The wide distribution of ABB with trace amounts of Bchl and with versatile energy-transducing systems may be the result of adaptation to various environments, from phototrophic bacteria to strictly aerobic (nonphototrophic) bacteria or denitrifying bacteria.

Thus, ABB isolated from Australian marine environments are similar to the aerobic photosynthetic bacteria (e.g., *R. denitrificans*) from Japan with respect to the biochemistry and physiology of the bacteria, such as the presence of Bchl and photochemical activities (16). However, the phylogenic relationship between *R. denitrificans* and ABB in Australia has not been investigated. More research is necessary to determine the similarities and differences between the strains from Australia and Japan and to explain why the ABB are very prevalent in some Australian habitats.

ACKNOWLEDGMENTS

We thank B. Hatcher and his colleagues for their kind help and critical discussions during our research in Western Australia. We also thank T. Done of the Australian Institute of Marine Science and J. Kuo of the University of Western Australia, J. Mellors of the Northern Fisheries Research Center, and K. Edyvane of the James Cook University of North Queensland for the identification of seaweed, seagrasses, and corals. Many staff at the Australian Institute of Marine Science helped us during our stay in Australia.

We thank D. Hopley of the James Cook University for permitting us to use the university facilities. We thank D. Moriarty of CSIRO, Brisbane, and J. Fuerst of the University of Queensland for permitting us to use their laboratories.

This study was supported by a grant from the International Scientific Research Program (no. 01041070) and a grant on Priority Area "The molecular mechanism of photoreception" (no. 01621003) of the Japanese Ministry of Education, Science and Culture.

REFERENCES

1. **Arata, H., Y. Serikawa, and K. Takamiya.** 1988. Trimethylamine *N*-oxide respiration by aerobic photosynthetic bacterium, *Erythrobacter* sp. OCh 114. J. Biochem. **103**:1011–1015.
2. **Bauld, T., L. A. Chambers, and G. W. Skyring.** 1979. Primary productivity, sulfate reduction and sulfur isotope fractionation in algal mats and sediments of Hamelin Pool, Shark Bay, Western Australia. Aust. J. Mar. Freshwater Res. **30**:753–764.
3. **Clayton, R. K.** 1963. Absorption spectra of photosynthetic bacteria and their chlorophylls, p. 495–500. *In* H. Gest, A. San Pietro, and L. P. Vernon (ed.), Bacterial photosynthesis. Antioch Publishing Co., Yellow Springs, Ohio.
4. **Dill, R. F., E. A. Shinn, A. T. Jones, K. Kelly, and R. P. Steinen.** 1986. Giant subtidal stromatolites forming in normal salinities waters. Nature (London) **325**:55–58.
5. **Dravis, J. J.** 1983. Hardened subtidal stromatolites, Bahamas. Science **219**:385–386.
6. **Harashima, K., M. Nakagawa, and N. Murata.** 1982. Photochemical activities of bacteriochlorophyll in aerobically grown cells of aerobic heterotrophs, *Erythrobacter* species (OCh114) and *Erythrobacter longus* (OCh 101). Plant Cell Physiol. **23**:185–193.
7. **Harashima, K., and K. Takamiya.** 1989. Photosynthesis and photosynthetic apparatus, p. 39–72. *In* K. Harashima, T. Shiba, and N. Murata (ed.), Aerobic photosynthetic bacteria. Springer-Verlag, Berlin.
8. **Moore, L., B. Knott, and N. Stanley.** 1984. The stromatolites of Lake Clifton, western Australia. Search **14**:309–314.
9. **Moriarty, D. J. W.** 1983. Bacterial biomass and productivity in sediments, stromatolites, and water of Hamelin Pool, Shark Bay, Western Australia. Geomicrobiol. J. **3**:121–133.
10. **Okamura, K., K. Takamiya, and M. Nishimura.** 1986. Photosynthetic electron transfer system is inoperative in anaerobic cells of *Erythrobacter* species strain OCh 114. Arch. Microbiol. **142**:12–17.
11. **Playford, P. E.** 1980. Environmental controls on the morphology of modern stromatolites at Hamelin Pool, Western Australia, p. 73–77. Western Australia Geological Survey Annual Report (for 1979). Benbow Publishing Co., Perth, Western Australia.
12. **Sato, K.** 1978. Bacteriochlorophyll formation by facultative methylotrophs, *Protaminobacter ruber* and *Pseudomonas* AM 1. FEBS Lett. **85**:207–210.
13. **Shiba, T.** 1984. Utilization of light energy by the strictly aerobic bacterium, *Erythrobacter* sp. OCh 114. J. Gen. Appl. Microbiol. **30**:239–244.
14. **Shiba, T.** Syst. Appl. Microbiol., in press.
15. **Shiba, T., and K. Abe.** 1987. An aerobic bacterium containing bacteriochlorophyll-proteins showing absorption maxima of 812, 844 and 862 nm. Agric. Biol. Chem. **51**:945–946.
16. **Shiba, T., and K. Harashima** 1986. Aerobic photosynthetic bacteria. Microbiol. Sci. **3**:376–378.
17. **Shiba, T., and U. Shimidu** 1982. *Erythrobacter longus* gen. nov., sp. nov., an aerobic bacterium which contains bacteriochlorophyll *a*. Int. J. Syst. Bacteriol. **32**:211–217.
18. **Shiba, T., U. Shimidu, and N. Taga.** 1979. Distribution of aerobic bacteria which contain bacteriochlorophyll *a*. Appl. Environ. Microbiol. **38**:43–45.
19. **Shioi, Y.** 1986. Growth characteristics and substrate specificity of aerobic photosynthetic bacterium, *Erythrobacter* sp. (OCh 114). Plant Cell Physiol. **27**:567–572.
20. **Shioi, Y., M. Doi, H. Arata, and K. Takamiya.** 1988. A denitrifying activity in an aerobic photosynthetic bacterium, *Erythrobacter* sp. strain OCh 114. Plant Cell Physiol. **29**:861–865.
21. **Taga, N.** 1968. Some ecological aspects of marine bacteria in the Kuroshio current. Bull. Misaki Mar. Biol. Inst. Kyoto Univ. **12**:56–76.
22. **Takamiya, K., H. Arata, Y. Shioi, and M. Doi.** 1988. Restoration of the optimal redox state for the photosynthetic electron transfer system by auxiliary oxidants in an aerobic photosynthetic bacterium, *Erythrobacter* sp. OCh 114. Biochim. Biophys. Acta **935**:26–33
23. **Takamiya, K., and H. Hanada.** 1980. Cytochrome b_{560} in chromatophores from *Chromatium vinosum*. Plant Cell Physiol. **21**:979–988.
24. **Wilkinson, C. R.** 1980. Cyanobacteria symbiotic in marine sponges, p. 553–563. *In* W. Schwemmler and H. Schenk (ed.), Endocytobiology: endosymbiosis and cell biology. Walter de Gruyter, Berlin.