

Room:301A

Time:May 26 14:15-14:45

# Phycological perspective on evolution of life and earth environment

Isao Inouye<sup>1\*</sup>

<sup>1</sup>Life and Env.Sciences, Univ. Tsukuba

Oxygenic photosynthesis first appeared in cyanobacteria (blue green algae) should have been a key evolutionary event that caused irreversible changes to earth's environment and determined fate of subsequent evolution of life. Evolution and diversification of algae (cyanobacteria and eukaryotic autotrophs excluding land plants) as primary producers resulted in increase of oxygen concentration in the ocean and atmosphere, which may have led to the evolution of eukaryotic organisms and eventually to the evolution of multicellular organisms. As compared with early ecosystem of prokaryotes, scale of primary production should have expanded millions times before the beginning of the Paleozoic era up to the level that can feed multicellular organisms in the ecosystem of Cambrian explosion. Since the Paleozoic, the green plants have been major producers on land. In contrast, primary producers changed to new groups of algae called secondary plants (algae evolved via multiple endosymbioses between heterotrophic eukaryotes and eukaryotic algae). Secondary plants have been playing significant roles in global ecosystem and carbon cycle since the Mesozoic.

Keywords: algae, oxygenic photosynthesis, eukaryotic organisms, endosymbioses, secondary plants, global ecosystem



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# Evolution of the photosynthetic life

Takeshi Nakayama<sup>1\*</sup>

<sup>1</sup>University of Tsukuba

The plants (land plants and algae) play important roles in the evolution of earth environment through the oxygenic photosynthesis. The oxygenic photosynthesis was acquired only once by cyanobacteria, and transferred to eukaryotes via primary endosymbiosis. In addition, various plants such as diatoms originated via secondary and tertiary endosymbioses. The "plantize" by symbiosis are not only past events, but also progressive events. In addition, some plants lost photosynthetic ability. These complicated evolutionary events of plants generate and maintain the present environment of earth.

Keywords: endosymbiosis, algae

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BBG021-03

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Time:May 26 15:00-15:15

# Ongoing process of plastid acquisition in dinoflagellates

Haruyo Yamaguchi<sup>1\*</sup>, Isao Inouye<sup>2</sup>

<sup>1</sup>NIES, <sup>2</sup>University of Tsukuba

Dinoflagellates, comprising about 2,000 species, exhibit remarkable diversity in terms of morphological and ecological properties. It is known that the dinoflagellates acquired their plastid via secondary endosymbiosis so that they are called secondary plants. However, about a half of known species lost their photosynthetic ability secondarily, and turned back to heterotrophic life forms. In the present-day ocean, photosynthetic dinoflagellates are important as primary producers together with diatoms and coccolithophorids, while heterotrophic ones play a significant role as primary consumers in microbial loop (or microbial food web).

It is known that some heterotrophic dinoflagellates again turned back to photosynthetic by acquiring new plastids via "tertiary endosymbioses". The tertiary endosymbioses are endosymbiotic evolutionary events between the secondary plants and dinoflagellates. Two types of tertiary endosymbioses are known: one is that the plastid is of haptophyte origin (e.g. *Karenia*) and the other diatom origin (e.g. *Durinskia*). The tertiary plastids appropriately work in the dinoflagellate cell as integrated organelles, and they are equally inherited to daughter cells, as are conventional plastids.

The tertiary endosymbiosis should begin by predating a secondary plant. Possible intermediate states between a simple predation and an established tertiary plastid are known in the dinoflagellates. Studies on such dinoflagellates would improve our understanding on evolutionary process of plastid acquisition. I will introduce six dinoflagellate species that would exhibit different evolutionary states of plastid acquisition. These dinoflagellates engulf cryptophytes from outside the cell and temporarily retain their chloroplasts (sometimes with their other organelles) within the cell. Such temporary plastids (symbionts) are called as "kleptochloroplasts (stolen chloroplasts)". Specificity between the host and symbiont and residual components of the symbionts are different among species, probably reflecting different states of evolution from preys to integrated plastids. Comparisons of these possibly different states of evolution would provide insights to understand the process of plastid acquisition, and future genome analyses on these dinoflagellates would improve our understanding further.

Dinoflagellates are an algal group that has prospered at least since the Mesozoic era onward. The dramatic changes on manners of nutrition may involve their prosperity. Dinoflagellate cysts remain as microfossils in sediments and are common targets of stratigraphy of the Mesozoic and Cenozoic.

Keywords: algae, dinoflagellate, tertiary endosymbiosis, kleptochloroplast



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Plasticity of eukaryotic genomes: The proteomes of dinoflagellate plastids as a case study

Yuji Inagaki<sup>1\*</sup>

<sup>1</sup>Univ. Tsukuba

There is no doubt that the endosymbioses of alpha-proteobacterium and cyanobacterium, which gave rise to mitochondria and plastids, respectively, had great impacts on eukaryotic genome evolution. As the extent organelle genomes are extremely reduced comparing to their free-living relatives, the vast majority of endosymbiont genes became dispensable for the lifestyle in a eukaryotic cell and were eventually discarded. On the other hand, the genes, which are essential for functions and maintenance of endosymbionts/organelles, were transferred to the host (eukaryotic) genome. According to the "gene flow" from the endosymbiot to host genomes (endosymbiotic gene transfer or EGT), bacterial genes – those with specific affinities to the bacterial homologs – encoded in eukaryotic genomes have been considered as the results of EGT. In this presentation, I discuss the origins of nucleus-encoded, plastid-targeted genes in dinoflagellates that experienced plastid exchange, and the putative plasticity of eukaryotic genomes: Eukaryotes most likely have the ability to integrate foreign genes not only from their endosymbionts, but also diverged organisms, which were involved in neither acquisition of mitochondrion nor plastid.

Keywords: eukaryotes, genome evolution, endosymbiosis, dinoflagellates, plastids, proteome



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# Dynamics of algal evolution represented by micropaleontological research

Itsuki Suto1\*

<sup>1</sup>Dpt. Earth & Planet. Sci., Nagoya Univ.

0) Fossil research to know evolution

There is no method to know actual biological evolution without researching fossils, alt-hough most investigation has been held by phylogenic methods. Concerning diatom, there are evolutional studies of fossil species by Yanagisawa & Akiba and report about its valve-size reduction by Finkel et al. (2005) as examples. However, there is hardly any fossil study directly connecting with modern species and its ecology. Therefore, the author will introduce a taxonomic study of fossil diatom genus <u>Chaetoceros</u>, its evolutional event affected by geological and oceanic changes, and the influence to other marine organisms in this presentation. For suchlike studies, it is important to combine ecological information of living species and detail geological one of fossil, cross-cutting collaboration will be needed.

#### 1) Importance of Chaetoceros resting spore studies

The marine diatom genus <u>Chaetoceros</u> is one of the most important taxa in present oceans, especially coastal upwelling regions (Hasle & Syvertsen, 1996). Under nutri-ent-rich conditions, most species reproduce rapidly and form long chains of thin-walled cells, but their valves are not preserved as fossil due to dissolution (Itakura, 2000). On the other hand, as nutrient supplies are depleted, most of them form thick-walled resting spores which sink to the sea floor where they await the return of favorable conditions (McQuoid & Hobson, 1996). The heavily silicified resting spore valves are preserved in sediment as fossils and abundantly occurred from near-shore sediments in association with other fossil diatom valves, therefore, they can provide useful information for recon-structing paleoproductivity and paleoenvironmental changes.

2) Chaetoceros Explosion Event across the Eocene/Oligocene boundary

The taxonomy of resting spores is less well understood because its vegetative frustules are rarely preserved with the spores and their valve structures are simple. No attention, therefore, has been paid to the significance of resting spores from a geological point of view, which contrast well with that the taxonomy and biostratigraphy of fossil dia-toms from Cenozoic sediments have been studied intensively in several oceans by using marine sedimentary successions collected by the DSDP, ODP and IODP.

Recently, a firm taxonomic basis of fossil resting spores formed in biostratigraphic and paleoceanographic research, using Eocene through the Recent samples (e.g. Suto, 2006). As the result, distinct resting spore event (<u>Chaetoceros</u> Explosion Event, CEE), including abrupt increasing of species richness and abundance, and reducing valve sizes was documented from the sediments collected in Norwegian Sea within a ~6 myr time interval across the Eocene/Oligocene boundary (Suto, 2006, Suto in prep.).

Based on evaluation of the ecologic differences between <u>Chaetoceros</u> and cyst-forming dinoflagellates, Suto (2006) indicated that i) the role of main primary producer might have switched from dinoflagellate in the Eocene to diatom, especially <u>Chaetoceros</u>, in the Oligocene; ii) the conditions in the Norwegian Sea changed from stable with a constant (annual) nutrient supply provided by upwelling in winter in the Eocene, to unstable with a sporadic supply of nutrients by increased vertical mixing in the Ocean after the development of Antarctic Circumpolar Current leading enhanced nutrient supply to the surface waters (Falkowski et al., 2004).

The CEE event was also recognized in the DSDP Holes 366 and 369A, eastern equa-torial Atlantic Ocean (Suto, in prep.), the event, therefore, might occur in all over the world oceans. Moreover, the evolution of the Mysticeti (baleen whales), which consumes a lot of copepods mainly eating diatoms, from the Archaeoceti (paleowhale) across the Eo-cene/Oligocene boundary, coincides with CEE. Consequently, CEE is likely to have en-hanced the evolution of whales (<u>Chaetoceros</u>-baleen whale co-evolution hypothe-sis)(Suto presented in AGU, 2007).

Keywords: diatoms, micropaleontology, paleoceanography, evolution, Eocene/Oligocene Boundary, algae

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### Symbiosis between foraminifer and red algae.

Akiko Yokoyama1\*

<sup>1</sup>Grad. Sch. Life Env. Sci., Univ. Tsukuba

Large benthic foraminifera and some planktonic foraminifera have photosynthetic endosymbionts in their cytoplasm. These symbionts are cyanobacteria, diatoms, green algae, dinoflagellates, red algae and haptophytes. Each taxonomic group of the host foraminifera has a different taxonomic group of algal endosymbiont, furthermore there are few algal symbiont species. The unicellular red alga *Porphyridium purpureum* was identified as an endosymbiont of a Peneroplidaean foraminifer based on its color and ultrastructure (Lee 1990). Some symbionts can be isolated and maintained as clonal cultures. To evaluate the taxonomic and phylogenetic position of the *Porphyridium* symbionts, SSU rDNA sequences were done. All the *Porphyridium* symbionts were monophyletic and distinct from the clade of free-living *P. purpureum* collected from terrestrial habitats. Moreover, some physiological properties of the symbionts were also different from those of free-living isolates. These results suggested that symbionts of peneroplid foraminifers comprise an entity distinct from typical *P. purpureum*.

Phylogenetic analysis of the host foraminifera was performed using SSU rDNA sequences showed that all foraminifers having *Porphyridium* endosmbionts are monophyletic. Therefore I propose that the Porphyridium- foraminifer endosymbiosis arose only once.

Keywords: Foraminifer, Microalgae, Red algae, symbiosis, Peneroplidae, Porphyridium



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# Environmental factors that enhance or collapse foraminifer-microalgal symbiosis

Kazuhiko Fujita<sup>1\*</sup>

 $^1 \mathrm{University}$  of the Ryukyus

Algal symbionts-bearing large benthic foraminifers are known as prolific primary and carbonate producers in coral-reef associated environments at the present and geological times. Understanding the mechanism of foraminifer-microalgal symbiosis is necessary to clarify their responses to secular variations in the Earth system, paleoceanographic changes, and future global environmental changes. Here I reviewed environmental factors that enhance or collapse the foraminifer-microalgal symbiosis. Negative factors which reduce net primary production of algal symbionts and the growth of a foraminiferal host include extremely high and low temperature, low pH, stagnant water motions and high nutrient concentrations. On the other hand, positive factors which enhance net primary production and calcification are poorly known. Our new culturing results indicated that higher pCO<sub>2</sub> enhanced the calcification of symbiont-bearing hyaline taxa due to enhanced photosynthetic activity of the symbionts under high pCO<sub>2</sub> seawater. Future culturing experiments under unrealistic seawater chemistry will give new insights into the mechanisms of foraminiferal-microalgal symbiosis.



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### Establishment and breakdown of symbiosis between corals and zooxanthellae

Kazuhiko Koike1\*, Hiroshi Yamashita1

#### <sup>1</sup>Graduate School of Biosphere Science

Enormous numbers of symbiotic dinoflagellates (zooxanthella or genus Symbiodinium) are engaged in scleractinian corals in tropical seas. They are seemingly mutualistic; Corals rely on the organic materials from the symbionts, and the symbionts do on the inorganic nutrients and carbonates from the corals. This close relationship has been passed down unbroken from Triassic and been firmly grounded on their evolutions. However, they might be rather independent.

Coral harbors symbiont intracellularly. Most of the coral species acquire symbionts not maternally but from environments. In this case, they must at least select the symbionts from other suspending particles in seawater, and keep them in their cells. How? Lively discussions have been done on this topic so far, and as yet not been brought to a conclusion. We consider this event is involved in some chemical recognition by a lectin, a carbohydrate-recognizing protein. Lectins from corals bind to the free-swimming zooxanthellae, and other non-symbiotic microalgae, but then, reverse reactions occurred; soon the zooxanthella deformed into spherical form and lost mobility as it were arrested, but still maintained active growth. On the other hand, non-symbiotic algae bust or aggregated and non-growthable anymore. Recently, Dr. M. Jimbo, Kitasato University, found that artificially removal of surface carbohydrate structure on the zooxanthella significantly retarded the establishment of symbiosis with corals. In this connection we may add that zooxanthellae in free-swimming form possess flagella and a well-developed eye-spot. But after symbiosis with animals, they lose these organella. Of course they may not need foot and eye in animals, that would be, but it seems host-directed mechanisms might control the failure of these formations in the symbionts, and if it is, this should be another arresting mechanism by corals.

Another particular interest to the symbiont acquisition by corals would be a presence of the symbiont-sources in the environment. According to our previous analysis by using quantitative PCR, at maximum several hundred thousand cells were existing in 1 L of seawater at a coral reef. Subsequent analyzes of environmental DNA clones and culture strains isolated from ambient waters or sands revealed; zooxanthellae never engaging to the animal-bearing lineage were in the environment, and contrarily those exactly much to the subsidiary engagement to animals were also. We still do not know the symbiotic implication of the former group (it should be very interesting when considering the symbiont evolution), but can suspect the latter group might be derived from ambient corals.

Next we performed an experiment to know whether corals actually release symbionts to the water. Healthy corals in an aquarium indeed discharged the symbionts at accurate periodicity. Corals in field also discharge them to a bottle attached to the branch. Based on the qPCR quantifications, ca. 6000 cells/h were released from just 1 cm2 surface of the coral, and interestingly, a certain type of genetic clade (clade C) was alternatively discharged ahead of another clade (clade D) which is recognized as thermally tough clade. This phenomenon might be interpreted as a survival strategy of corals suffering to rapid environmental changes, such as global warming.

Symbionts may thus be arrested by corals and eventually dismissed for corals' reason. Their relationship is mutualistic as a result, but corals are somehow selfish.

Keywords: Symbiodinium, coral, zzooxanthella



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Mass extinction of photosynthetic organisms and environmental perturbation caused by an impact at the K/Pg boundary

Sohsuke Ohno<sup>1\*</sup>, Kazuhisa Goto<sup>1</sup>

<sup>1</sup>Chiba Institute of Technology

We review geoogic records of the mass extinction at the K/Pg boundary and the hypotheses of the environmental perturbation caused by the impact. We also try to assess the infulence of the impact on photosynthetic organisms and its ecosystem.

Keywords: impact, mass extinction, K/Pg boundary, environmental perturbation

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BBG021-10

Room:301A

Time:May 26 17:00-17:30

# Paradigm shift of primary producers of the Oceans

Hideaki Miyashita1\*

<sup>1</sup>Kyoto University

Phototrophs carry out the light-induced electron flow, and synthesize organic compounds using the resulted proton-electrochemical potential gradient across the membrane. Ecosystem depends its energy on the organic compounds produced by phototrophs. The phototrophs are, therefore, the starting point of energy flow into the ecosystem. Marine ecosystem takes about a half of global primary production accounting for ca. 50 gigatons of carbon per year. For a long time, it was believed that diatom and flagellated phytoplankton were responsible for the marine primary production. However, recent improvements and developments of HPLC detection technique for photosynthetic pigments, molecular detection technique for microbes, flowcytometry, metagenome analysis and so on revealed following discoveries;

1) Picocyanobacteria including Synechococcus and Prochlorococcus are widely and significantly distribute over the ocean surface (1-3).

2) Bacteriochlorophyll a-containing aerobic anoxygenic photosynthetic bacteria are widely and significantly distribute over the ocean surface (4).

3) Proteorhodopsin-containing bacteria are widely and significantly distribute over the ocean surface (5).

4) Eukaryotic picophytoplankton are widely and significantly distribute over the ocean surface (6,7).

5) Diverse of chlorophylls could be detected in the sediment core samples (8).

These discoveries suggest that the starting point of energy flow in the marine ecosystem is not only the microalgae such as diatom and flagellated phytoplankton but also diverse phototrophs.

In this presentation, I would like to discuss the paradigm shift of the understanding of marine primary producers which had been treated as black box.

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Keywords: photosynthesis, cyanobacteria, microalgae, bacteriochlorophyll, proteorhodopsin, solar radiation



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# Biodiversity of eukaryotic picoplankton

Masanobu Kawachi<sup>1\*</sup>

<sup>1</sup>National Institute for Environmental Stu

not yet

Keywords: picoplakton, biodiversity, phylogeney



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# Viral impacts on algal blooms: quantitative and qualitative effects

Nagasaki Keizo<sup>1\*</sup>

<sup>1</sup>Fisheries Research Agency

Recently, an increasing number of viruses infectious to bloom-forming microalgae are isolated and characterized. In this paper, significance of their ecological roles is mainly introduced. HcRNAV is a polyhedral virus infecting the bivalve-killing dinoflagellate Heterocapsa circularisquama, which harbors a linear 4.4-kb ssRNA genome. In the RdRp sequence tree, this virus fell into a phylogenetic clade which is distant from any other virus ever reported so far; just recently approved as the typical species of a new genus "Dinornavirus" by the International Committee on Taxonomy of Viruses (ICTV). Based on a field survey for more than six years in Ago Bay, Japan, an intimate ecological relationship between the host and the virus was elucidated. HcRNAV population is composed of multiple types which differ in intraspecies host specificity; i.e., differing in strain-specific infectivity among them; on the other hand, the host is composed of distinctive types differing in virus sensitivity spectra. Thus, virus infection can change clonal composition of the host population. Results of genome comparison supported the hypothesis that the nanostructural difference on the viral surface among these types is crucial for determining the specificity. We assume that the type variations of H. circularisquama and its viruses are more complicated than we suspect in natural environments. The host algal population dynamics is apparently affected by HcRNAV infection; viral impact on the algal population is considered to be not only quantitative (on biomass) but also qualitative (on clonal composition).

Keywords: virus, microalgae, algal bloom, aquatic ecology



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### Responses of phytoplankton and heterotrophs in open oceans to nutrient supply

Koji Suzuki<sup>1\*</sup>, Atsushi Tsuda<sup>2</sup>

<sup>1</sup>Hokkaido University, <sup>2</sup>University of Tokyo

Many elements are required for the photosynthesis and growth of phytoplankton. However, Liebig's law of the minimum states only one element limits the growth of organisms at any given time. Here we briefly introduce the behavior of limited nutrients for phytoplankton in the sea, and the responses of not only phytoplankton, but also heterotrophs in open waters, especially the western North Pacific, to nutrient additions. In the subarctic western North Pacific, ample amount of nutrients are supplied from deeper layers to the surface through winter mixing. From spring to summer, phytoplankton growth is stimulated by increases in solar radiation and stratification of the water column. However, levels of chlorophyll (Chl) a, an indicator of phytoplankton biomass, in this region during summer are lower than expected from surface nitrate concentrations. Hence, the subarctic western North Pacific has recently been recognized as one of the HNLC (high nitrate, low Chl) regions, where iron (Fe) availability in seawater is often very low, because of low Fe solubility in seawater and low Fe supplies from land. To verify Fe deficiency in phytoplankton assemblages in this region, two in situ Fe fertilization experiments, SEEDS and SEEDS-II, were carried out in summers of 2001 and 2004, respectively. The large chain-forming centric diatom Chaetoceros debilis dramatically bloomed after Fe enrichment during SEEDS, while small phytoflagellates such as green algae and cryptophytes flourished with a small magnitude during SEEDS-II. The causes of the different responses of phytoplankton between the two experiments could be due to: 1) high grazing pressure of mesozooplankton during SEEDS-II, and 2) a dilution of bioavailable Fe by deeper mixed layer in SEEDS-II, resulting in continued Fe deficiency in large diatoms. Increases in bacterial productivity were also observed even in SEEDS-II, although apparent dissolved organic carbon concentrations little changed. From the results of the two in situ Fe enrichment experiments, it has become evident that Fe availability controls the ecosystems and biogeochemical processes in the subarctic western North Pacific. On the other hand, in the tropical and subtropical western North Pacific, permanent pycnocline has well developed throughout the year, resulting in the depletion of surface nitrate. In such conditions, pico-sized autotrophic cells, which have advantage in nutrient uptake because of their high surface area to volume ratios, become dominant in the phytoplankton assemblages. Recently, it has been pointed out that intensity of tropical cyclones including typhoon may have increased. During 1997-2007, total number of typhoon was 170, and 63% out of them induced substantial increases in Chl a level as estimated from satellite remote sensing. As a typical example, in fall 2003, Chl a concentrations increased by ca. 7 times after the passage of Typhoon Ketsana, which probably caused a strong upwelling in the sea. Relatively high concentrations of the Chl a continued for approximately 1 month. However, it is still unclear which phytoplankton species became dominant after typhoon passage. Effects of the phytoplankton assemblages increased by typhoon on the ecosystems and biogeochemical processes are also uncertain. Therefore, we conducted on-deck incubation experiments using the mixture of surface and subsurface waters in the areas on September 2007 and 2008. As common results of the experiments, levels of specific chemotaxonomic carotenoids probably derived from diatoms and chrysophytes increased after incubation. Our microscope observations also revealed that micro-sized diatoms such as *Pseudo-nitzchia seriata* complex increased. These results suggest that the enhancement of typhoon intensity may increase number of the blooms mainly consisted of diatoms in the tropical and subtropical North Pacific.

Keywords: limited nutrients, in situ iron fertilization experiments, typhoon disturbance



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# Dynamics and phototrophy of microbial communities in the ocean

Koji Hamasaki<sup>1\*</sup>, Yuki Sato<sup>2</sup>, Akito Taniguchi<sup>3</sup>

<sup>1</sup>AORI, The University of Tokyo, <sup>2</sup>Hokkaido University, <sup>3</sup>Kinki University

Possible role of phototrophy by heterotrohic bacterial populations on significant energy supply to oligotrophic ocean ecosystems has been recently suggested. Their ubiquitous distribution and unexpected abundance in surface seawater environments have been reportedly emphasized. Oxygenic photosynthetic bacteria, cyanobacteria, are one of the major primary producers in the ocean, whereas anoxygenic photosynthetic bacteria are rather minor in oxidized ocean environments because they are basically anaerobes and require reduced coumpounds as an electoron donners. Aerobic anoxygenic photosynthetic bacteria possessing an ability of photosynthetic light reactions under an aerobic condition were firstly isolated in 1979 by Shiba and colleagues. In 2000, Kolber and his colleagues reported that these photosynthetic bacteria widely distributed in oceanic surface seawaters and accounted for 11 % of total bacteria and 5-10 % of total chlorophyll a concentrations. Also, a wide distribution of some bacteria possessing light-dependent proton pump to generate ATP has been recently suggested. Some bacteria inhabiting marine surface waters possess rhodopsin-retinal complex to absorb light and carry proton ions across a cell membrane. This rhodopsin was just discovered ten years ago and named proteorhodopsin to distinguish from bacteriorhodopsin of archaeal homologous proteins. Both culture-dependent and -independent works indicated a ubiquitous distribution of proteorhodopsin-possessing bacteria in surface seawater environments. In this presentation, we would like to discuss spatiotemporal dynamics of these light-utilizing heterotrophic bacterial populations and possible effect of light and organic matter supply on their growth and survival in marine environments.

Keywords: marine bacteria, photosynthetic bacteria, rhodopsin, photoheterotrophy