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Carlos Pedrós-Alió

Department of Marine Biology and Oceanography, ICM, CMIMA-CSIC, Barcelona, Spain

Genomics and marine microbial ecology

Summary. Genomics has brought about a revolution in all fields of biology. Before the development of microbial ecology in the 1970s, microbes were not even considered in marine ecological studies. Today we know that half of the total primary production of the planet must be credited to microorganisms. This and other discoveries have changed dramatically the perspective and the focus of marine microbial ecology. The application of genomics-based approaches has provided new challenges and has allowed the discovery of novel functions, an appreciation of the great diversity of microorganisms, and the introduction of controversial ideas regarding the concepts of species, genome, and niche. Nevertheless, thorough knowledge of the traditional disciplines of biology is necessary to explore the possibilities arising from these new insights. This work reviews the different genomic techniques that can be applied to marine microbial ecology, including both sequencing of the complete genomes of microorganisms and metagenomics, which, in turn, can be complemented with the study of mRNAs (transcriptomics) and proteins (proteomics). The example of proteorhodopsin illustrates the type of information that can be gained from these approaches. A genomics perspective constitutes a map that will allow microbiologists to focus their research on potentially more productive aspects. [**Int Microbiol** 2006; 9(3):191-197]

Key words: genomics · marine microbial ecology · metagenomics · proteorhodopsin · phototrophy

Address for correspondence:
Departament de Biologia Marina i Oceanografia
Institut de Ciències del Mar, CMIMA-CSIC
Pg. Marítim de la Barceloneta, 37-49
08003 Barcelona, Spain
Tel. +34-932309597. Fax +34-932309555
E-mail: cpedros@icm.csic.es

Introduction

Neither genomics nor marine microbial ecology existed at the time of publication of *The Microbe's Contribution to Biology*. However, there is a parallel between the book's content and the current role of marine genomics: in both cases, the deeper knowledge of microbes served as an eye opener that revolutionized our understanding of life's possibilities. And, in both cases, there was an appreciation that all the disciplines of biology (biochemistry, genetics, physiology, taxonomy, etc.) would be simultaneously needed in order to exploit the knowledge that could be obtained by these new approaches.

The biological sciences are experiencing a revolution, both technical and intellectual, in good part due to the legacy left by the human genome sequencing project [21], for example, the fact that biology is being transformed from a data-poor into a data-rich science. The ever-growing number of sequences allows biologists to ask new questions and to approach the old ones from a more-informed perspective. The questions that can be formulated now go beyond pure genetics (in the sense of genome organization or diversity and the phylogeny of life) and include both the functioning of living beings as a whole and their adaptation to the environment. In fact, getting sequences is no longer a problem. Instead, the key issue is to use one's imagination to ask the most interesting questions that the available data can answer.

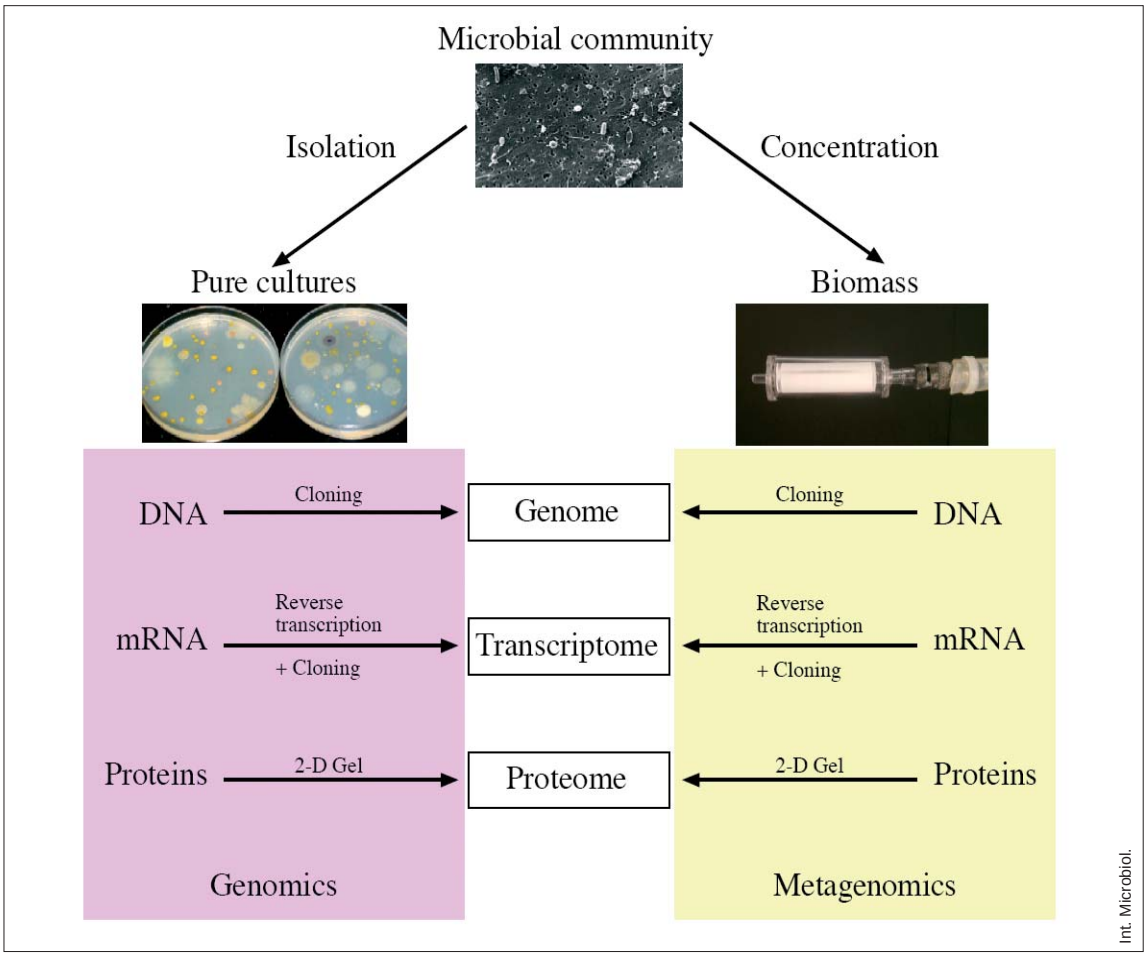

Fig. 1. Molecular and genomic approaches to the study of natural communities of microorganisms. Left: Particular microorganisms can be isolated in axenic cultures. In this case, it is relatively straightforward to sequence a gene, to study a particular mRNA, or to look for a protein. Right: The same three possibilities apply to the study of the entire microbial community. In classical molecular microbial ecology, one gene is studied at a time. In genomics, the entire genome of an axenic culture or the entire metagenome (all the genomes in a community) is analyzed at the same time. (Picture credits: SEM by Carlos Pedrós-Alió; Petri dishes by Laura Gómez-Consarnau; Filter by Fernando Unrein.)

Modern marine microbial ecology can be considered to have started in the 1970s, when it was shown that most respiration in the oceans was in the bacterial size fractions [16] and that bacteria were very abundant [9,23]. Before that time, microbes were not even considered in the ecology of the oceans. Nowadays, however, marine microorganisms are known to be responsible for half of the total primary production on the planet [5], and the 10^{30} microbial cells present in the oceans [22] account for more than 95% of the total respiration [2]. The change of perspective, therefore, has been spectacular.

The application of genomic approaches to marine microbial ecology in the past few years has caused a kind of Copernican revolution. Thanks to such techniques, novel functions have been discovered, a large diversity of microorganisms has been uncovered, and the meaning of concepts such as species, genome, and niche has been challenged [3]. This article reviews the different genomics-based approaches relevant for marine microbial ecology and uses one example from each to demonstrate their tremendous possibilities.

From genes to genomes: a change of scale

Figure 1 shows a flowchart of the different ways in which molecular techniques can be used in marine microbial ecology. On the right half of the graph, the entire biomass of the community is analyzed. In the past, molecular techniques had been used to study single genes. For example, DNA from a natural sample would be screened for the genes coding for 16S rRNA—this would reveal the diversity of the microor-

ganisms in the sample—or, the presence of a certain gene (such as *nif*, the gene for nitrogen fixation) could be determined. Certain messenger RNAs can be analyzed by reverse transcription to DNA and subsequent cloning. In this case, the technique will confirm not only that the corresponding gene is there, but also that the gene is being expressed actively. Finally, particular proteins can be searched for. This is more difficult to do in natural samples, because proteins cannot be amplified by PCR as nucleic acids can. However, if a protein is sufficiently abundant, there is no reason why it cannot be purified from the environment. This would evidence that the gene is present, that it is being expressed, and that the corresponding protein is being synthesized at the particular place and time where the sample was originally taken.

The left half of Fig. 1 shows the equivalent approaches when a microorganism has been previously isolated in axenic culture. In this case, all the techniques are easier to carry out, because the organism can be grown to high concentrations, and because most genes will be represented by a single copy (since there will be a single species). The problem is that isolation in axenic culture is a selective process that only retrieves some of the microbes that are important in nature [13,14].

The same figure can be used to illustrate genomic approaches to marine microbial ecology. The only difference that genomics introduces is that of scale. In the left part of the figure, the entire genome of the organism will be sequenced instead of only one gene. In the right part of the figure, all the genomes of all the organisms present in the sample (the metagenome) will be sequenced. The study of genomes (genomics in the case of single microbial species or metagenomics in the case of whole communities) can be complemented with the study of the mRNAs (transcriptome, transcriptomics) or proteins (proteome, proteomics). Obviously, this change of scale requires two things: a large sequencing capacity and very powerful bioinformatics tools to organize and study the massive amount of information. Both these things received a decisive impulse with the human genome sequencing project, and the sequencing capabilities and bioinformatics resources that resulted from it are now widely available.

Genomic approaches to marine microbial ecology

This section will review the different approaches available to study DNA (genomics and metagenomics). Consideration of either transcriptomics or proteomics exceeds the scope of the present paper. Some approaches to study DNA are summarized in Fig. 2.

Genomics of marine microorganisms isolated in axenic culture (Fig. 2A). Until one year ago, most sequenced genomes belonged to bacteria of medical interest. However, thanks to the initiative of the Gordon and Betty Moore Foundation, over 150 genomes of marine bacteria have been sequenced in the last two years [http://www.moore.org/program_areas/science/initiatives/marine_microbiology/initiative_marine_microbiology.asp]. Of course, the main caveat is that many of the bacteria isolated in axenic culture are not the most important in nature. However, these genomes offer a wealth of information that can be used to interpret the results from transcriptomics and proteomics. For example, the complete genomes of four cyanobacteria have offered novel insights into the meaning of concepts such as species and ecological niche.

Marine cyanobacteria are grouped into two closely related genera according to their 16S rRNA: *Prochlorococcus* and *Synechococcus*. It is estimated that these cyanobacteria are responsible for two thirds of the photosynthesis in the oceans, and they are widely distributed in the equatorial and temperate latitudes of all oceans. In fact, *Prochlorococcus* may be the most abundant photosynthetic organism on Earth [12]. Recently, the genomes of four different strains were sequenced: one from *Synechococcus* [11] and three from *Prochlorococcus* [4,17]. According to conventional 16S rRNA criteria, the three *Prochlorococcus* strains belonged to the same species. However, the genome of strain MIT9313 turned out to have 2.4 megabases (Mb), while those of the other two strains (MED4 and SS120) had only 1.7 Mb. It was very shocking to realize that organisms belonging to the same "species" may have genomes with such different sizes. Looking at the natural distribution of each strain, it could be appreciated that the size of the genome seemed to be related to the stability of the particular strain's environment. Thus, strain MED4 is adapted to live at the surface of the ocean, with relatively constant conditions of high light intensity and low nutrient availability, while strain SS120 is adapted to lower depths, where low light intensities and higher nutrient conditions are relatively constant. Strain MIT9313 inhabits intermediate depths, where conditions are likely to be more variable. The case of the *Synechococcus* strain is similar. It also has a 2.4-Mb genome and lives in upwelling and vertical mixing situations, where conditions are also more variable. Apparently, the two latter strains require an additional 0.7 Mb in their genomes to have enough versatility to survive in their changing environments. In effect, when genes conferring the ability to use different nitrogen sources were searched for in the four genomes, all were found to contain genes involved in the metabolism of ammonia. However, while the two strains with small genomes could only use one or two additional compounds, the two with a large genome could use

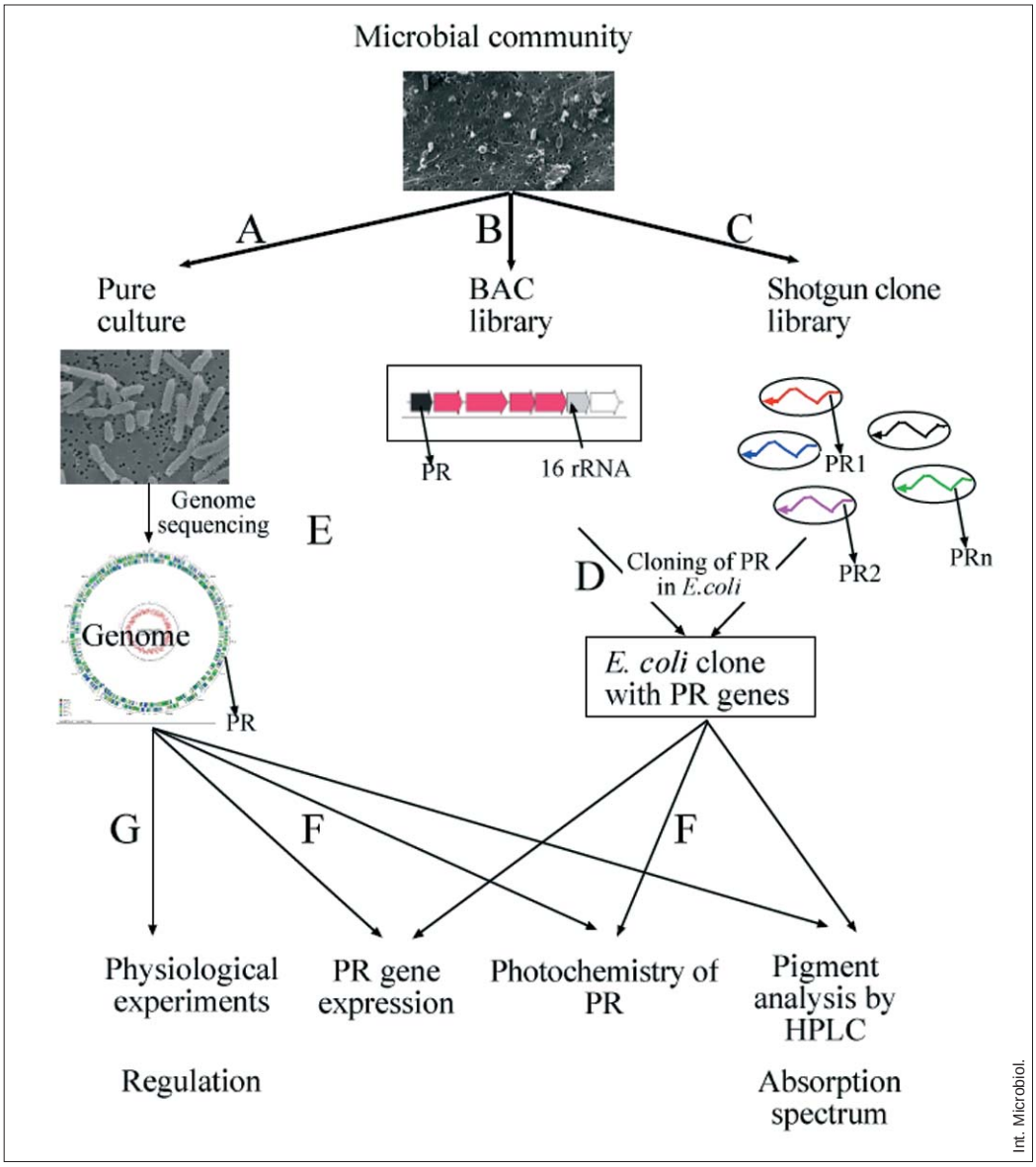

Fig. 2. Different approaches to environmental genomics. **(A)** An organism can be isolated in axenic culture. **(B)** Large fragments of the metagenome can be cloned in special vectors, such as BAC (bacterial artificial chromosome) or fosmid libraries, where the in vivo organization of the genes is preserved. **(C)** Small fragments can be shotgun cloned in conventional vectors. Sequencing is simpler but reassembly is more difficult in this case. **(D)** In order to study the function of any gene of interest, the gene needs to be cloned in *Escherichia coli*, since the approaches described in B and C only provide DNA sequences. **(E)** If an axenic culture is available, the entire genome can be sequenced and genes of interest can be identified. **(F)** In this way, a range of studies can be carried out in vivo. **(G)** Studies involving growth and regulation can only be carried out in organisms that have been isolated in axenic culture. (Picture credits: SEM of community by Carlos Pedrós-Alió; SEM of pure culture by Itziar Lekunberry.)

numerous sources of nitrogen, such as nitrate, nitrite, urea, amino acids, peptides, and even cyanate, a substance that had not been known to act as a nitrogen source for any microorganism. It therefore seems that the two strains adapted to constant environments discarded all the genes that were not strictly necessary for their growth, a phenomenon described as "genome streamlining" [8]. It is intriguing that evolution allows such major changes that affect full blocks of genes but which retain very similar 16S rRNA. In summary, the example of marine cyanobacteria demonstrates how genomic studies may dramatically alter our understanding of the taxonomy, evolution, physiology, and ecology of microorganisms.

Metagenomics (Fig. 2B and 2C). In one metagenomics approach, large fragments of environmental DNA can be carefully extracted and cloned in appropriate vectors, such as fosmids or BAC libraries (Fig. 2B). These large fragments of DNA (up to 100 kb) contain several genes arranged in the precise order in which they were found in the genome they came from. If a gene for 16S rRNA is found in one clone, the bacterium it came from can be identified and the neighboring genes can be sequenced. In this way, the existence of a novel function was discovered in an uncultivated bacterium. A clone from one such library had the 16S rRNA gene of SAR86 (a cluster of sequences retrieved from many oceans but with no representative in axenic culture). A gene coding for a protein similar to halorhodopsin was found in the same clone. Upon further study, this protein (named proteorhodopsin) was shown to use light to generate a proton gradient across the cell membrane; thus, an unknown group of bacteria, SAR86, was shown to have a novel function (phototrophy) [1].

An alternative metagenomics approach involves fragmenting the environmental DNA into small fragments (around 3 kb) and cloning those fragments in conventional vectors (Fig. 2C) in a procedure called "shotgun cloning." Accordingly, DNA fragments can be sequenced without previous screening. This allows for the discovery of novel genes regardless of their origin. The drawbacks are that this method requires massive sequencing to analyze the thousands of clones generated from a single sample, and that it is difficult to reassemble genomes from many small fragments. Nonetheless, by shotgun cloning a sample from the Sargasso Sea, Venter et al. [20] revealed over 100,000 genes, many of them with unknown functions. In one of the most typical examples, this strategy has increased by at least one order of magnitude the number of proteorhodopsin genes known from previous approaches.

New sequencing techniques are making metagenomic approaches cheaper and, therefore, accessible to most laboratories [6]. The sequencing technology offered by the 454 Life Sciences company, among others, is being used with increasing frequency. Although the sequenced fragments are, for the time being, very short (around 100 bases long) and this entails difficulties in the assembly of the fragments, the technique has been successfully used to sequence an entire bacterial genome in one week [10].

A third option is to use PCR with primers specific for a given group of bacteria or for a given gene, for example 16S rRNA. Then, the collection of sequences amplified can be subject to the same shotgun cloning and massive sequencing described above. Thus, Sogin et al. [18] have used this strategy, in combination with 454 sequencing, to screen deep-ocean samples for 16S rRNA genes. The addition of an amplification step and the enormous number of sequences that were subsequently generated have increased the known diversity of marine samples by one or two orders of magnitude over what was previously recognized from conventional cloning and sequencing. The large number of different sequences in one sample is in agreement with the idea that bacterial communities are formed by a few dozen abundant taxa and a very large collection of rare taxa, the former making up the diversity of that ecosystem and the latter contributing to its complete biodiversity [13,14].

Finally, if metagenomics libraries from two or more different communities are available, they can be used to compare the relative abundance of genes with given functions and these can be related back to the particular conditions in each environment. Tringe et al. [19], for example, compared libraries from the Sargasso Sea and whale falls in Antarctica. They could see that genes for chemotaxis were overrepresented in the whale fall communities. This suggests that chemotaxis is important for the bacteria to find and move towards the episodic whale fall in the bottom of the ocean. At the surface of the Sargasso Sea, by contrast, resources may be more regularly mixed by turbulence, making chemotaxis a less useful property. In any case, this comparison immediately suggests interesting ecological hypotheses that can be tested in further studies.

The return to general microbiology: the case of proteorhodopsin

A most welcome consequence of the revolution brought forward by genomics is the need to recover all the traditional disciplines of biology. In order to make sense out of the millions of basepairs of sequence, it is necessary to go back to the biochemistry textbooks to correctly interpret the metabolic pathways that can be reconstructed from genomes. It is also necessary to isolate more organisms in axenic culture and to characterize them with proper and careful taxonomy. And, of course, the tools and concepts of genetics are essential to try to understand how whole genomes function. Some of these aspects can be illustrated with the example of proteorhodopsins.

As mentioned earlier, proteorhodopsin (PR) was discovered through the large-fragment metagenomics approach (Fig. 2B). Small-fragment metagenomics increased by an order of magnitude the number of genes known to code for PRs found in natural samples (Fig. 2C). Up to this point, however, all that was available was the DNA sequence of one gene. But was this gene expressed? Did it code for active proteins? Did the protein confer any advantage to the bacteria

possessing it? Some of these questions could be answered by cloning the PR gene in *Escherichia coli* (Fig. 2D). Luckily, *E. coli* did express the gene and was able to put the protein to use (Fig. 2F). Upon illumination, the clones generated a proton gradient and this was only the case if light had the wavelength absorbed by retinal, the pigment in PR [1]. These biochemical and physiological studies would have been impossible if only the sequence were available. It was necessary to have the gene within a living cell, in this case an *E. coli* cell. However, in order to determine whether marine bacteria could use PR for faster or more efficient growth, axenic cultures of bacteria naturally having the gene were needed (Fig. 2A). After isolation in axenic culture and sequencing of the whole genome, Giovannoni et al. [7] showed that *Pelagibacter ubique*, one of the most abundant bacteria in the surface oceans, had the PR gene (Fig. 2E). With an axenic culture of a PR-containing bacterium, it became possible to do the biochemical and physiological studies carried out in *E. coli* in a more natural environment (Fig. 2F). Furthermore, the effects of PR on the growth of the organism could be analyzed (Fig. 2G). Giovannoni et al. [7] detected the formation of a proton gradient upon illumination with the appropriate wavelengths. But they could not show any difference in the growth of the organisms in the light or in the dark. Thus, the role of PR in natural bacteria remained a mystery.

At the Institut de Ciències del Mar, CSIC, in Barcelona, a large collection of bacteria had been isolated in axenic culture from the Blanes Bay Microbial Observatory (Fig. 2A). Nine of these bacteria were selected for the genome sequencing initiative of the Gordon and Betty Moore Foundation and several genomes became available at the end of 2005 (Fig. 2E). We concentrated our efforts on the three bacteroidetes representatives: *Leeuwenhoekiella blandensis* MED217 [15], *Dokdonia* sp. MED134, and *Polaribacter* sp. MED152 (Gómez-Consarnau et al., in preparation).

Upon analysis of their genomes, the presence of carotenoid genes was detected in all three isolates (Fig. 2F). This was expected, since the isolates were either yellow or orange. MED217 and MED134 had the genes *crt*(EBIY), necessary for the synthesis of β-carotene, and *crt*Z, necessary to convert β-carotene into zeaxanthin. In addition, strain MED152 had the genes *crt*D and *crt*A as well as an additional copy of *crt*Z. Since the axenic cultures were available, we could examine whether the two former strains were yellow and, using HPLC, whether the only carotenoids were β-carotene and zeaxanthin. Strain MED152 was orange and had an unidentified carotenoid in addition to β-carotene and zeaxanthin (Fig. 2F). This was obviously synthesized by the products of genes *crt*D and *crt*A, but the identity of this compound is still unknown.

The analysis of the three genomes also showed that strains MED134 and MED152 had two additional genes related to light: *blh*, a gene necessary to synthesize retinal from β-carotene, and the opsin gene. Thus, both the protein and the pigment that make up PR could be synthesized by these two strains. Thanks to the fact that axenic cultures are available, we can now check whether these genes are expressed in vivo (Fig. 2G). Preliminary experiments show promise to clarify the role of PR in natural marine bacterioplankton.

The finding of PR in marine bacteria indicates that a reinterpretation of bacterial heterotrophic activity in the sea may be in order. Measurements of this parameter have been traditionally carried out in the dark. If a substantial fraction of the community carries PR genes, however, measurements of carbon flow through bacteria may have been significantly underestimated. Out of the same amount of available dissolved organic matter, a microbial community rich in PR will produce more particulate organic matter than a community poor in PR, thus increasing the efficiency of carbon transfer in the microbial food web. I think this example nicely illustrates the rich interactions between genomics on the one hand and the traditional disciplines of biology on the other. The former acts as a map to guide the latter towards the most promising objectives and in the most effective way. The road ahead is tremendously exciting.

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Genómica marina y ecología microbiana

Resumen. La genómica ha supuesto una revolución en todos los campos de la biología. En la década de 1970, antes del desarrollo de la ecología microbiana, los microbios ni siquiera estaban presentes en los estudios de ecología marina. Hoy día sabemos que la mitad de la producción primaria total del planeta se debe a los microorganismos. Éste y otros descubrimientos han cambiado la perspectiva y el enfoque de la ecología microbiana marina. La aplicación de procedimientos basados en la genómica ha abierto nuevos retos y permitido descubrir nuevas funciones, a la vez que apreciar la gran diversidad de microorganismos. También ha facilitado la aparición de polémicas en torno a los conceptos de especie, genoma, y nicho. Sin embargo, es necesario explorar las posibilidades que presentan estos nuevos métodos, lo cual puede hacerse a través del conocimiento de las disciplinas tradicionales de la biología. Este trabajo examina las diversas técnicas genómicas que se pueden aplicar a la ecología microbiana marina, y que incluyen la secuenciación completa de microorganismos y la metagenenomica la cual, a su vez, se complementa con el estudio de mRNAs (transcriptómica) y proteínas (proteinómica). El ejemplo de la proteorrodopsina ilustra el tipo de información que puede obtenerse con estas aproximaciones. Una perspectiva genómica es como un mapa que permitirá a los microbiólogos enfocar su investigación en aspectos potencialmente más productivos. [**Int Microbiol** 2006; 9(3):191-197]

Palabras clave: genómica · ecología microbiana marina · metagenómica · proteorrodopsina · fototrofia

Genômica e ecologia microbiana marinha

Resumo. A genômica levou a uma revolução em todos os campos da biologia. Na década de 1970, antes do desenvolvimento da ecologia microbiana, os micróbios nem sequer estavam presentes nos estudos de ecologia marinha. Hoje em dia sabemos que a metade da produção primária total do planeta se deve aos microrganismos. Este e outros descobrimentos mudaram a perspectiva e o enfoque da ecologia microbiana marinha. A aplicação de procedimentos baseados na genômica abriu novos desafios, permitindo descobrir novas funções e ao mesmo tempo apreciar a grande diversidade de microrganismos. Também facilitou o surgimento de polêmicas em torno dos conceitos de espécie, genoma, e nicho. No entanto, é necessário explorar as possibilidades que apresentam estes novos métodos, o qual pode fazer-se através do conhecimento das disciplinas tradicionais da biologia. Este trabalho examina as diversas técnicas genômicas que podem ser aplicadas à ecologia microbiana marinha, e que incluem o sequenciamento completo de microrganismos e a metagenômica a qual, por sua vez, se complementa com o estudo de mRNAs (transcriptómica) e proteínas (proteômica). O exemplo da proteorrodopsina ilustra o tipo de informação que pode se obter com estas aproximações. Uma perspectiva genômica é como um mapa que permitirá aos microbiologistas focar sua pesquisa em aspectos potencialmente mais produtivos. [**Int Microbiol** 2006; 9(3):191-197]

Palavras chave: genômica · ecologia microbiana marinha · metagenômica · proteorrodopsina · fototrofia