Deep Sea Benthology
- History and Present State -

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1. INTRODUCTION

Earth is often referred to as the planet of water. 71% of the planet is covered by oceans, of which 75% belong to the so-called abyssal zone, with depths of 1000 m or more. In other words, the majority of the earth is oceans, and the majority of oceans are abyssal. However, we know so little about these vast areas that it is fair to call them an "unknown world." Our knowledge is particularly limited about the fauna living in these areas, their existence alone was only confirmed one century ago.

This review focuses on the ecological study of deep-sea benthos and gives an historical background of deep-sea benthology and presents a commentary on the state of research programs.

2. HISTORY OF DEEP SEA BENTHOLOGY

The following section reviews the research into abyssal benthos, referring to Horikoshi (1976), Mill (1983), Gage and Tyler (1991) and Fukushima (1995). The time periods mentioned in the following text were classified by the author for convenience.

(1) The Early Stage of Deep Sea Benthology

The initial research into abyssal fauna was a period of sampling and discovery. This period is characterized by the success in sampling fauna from the bathyal zone and the abyssal zone using non-quantitative sampling equipment (trawling, dredges, etc.).

The first recorded person to have sampled abyssal fauna is the British adventurer John Ross. In 1818 he succeeded in sampling basket stars from a depth of more than 1600 m in Baffin Bay in the Antarctic Ocean. He was followed by James Clark Ross, who in 1839 to 1843 discovered and reported abundant biotic communities at depths of around 1800 m in the Tasman Sea, again in the Antarctic (Gage and Tyler, 1991).

Reports of those samples confirmed the existence of organisms in the bathyal zone. Strangely, however, a counter theory known as the azoic zone, denied the existence of such organisms at the time. The azoic zone was a theory based on the results of dredging carried out by the Briton Edward Forbes in the Aegean Sea (1851 to 1854). It stated that organisms did not exist at depths greater than 600 m. Subsequently, Goodsir, Spitzbergen, Stars and others carried out sampling of fauna, but until the Challenger Expedition (1872 to 1876) which succeeded in collecting fauna from a depth of 5500 m, i.e. from the abyssal zone, there were repeated attempts and counter evidence concerning the azoic zone. Even after this argument seemed to be settled, up until the 1950s, surveys continued which challenged the discovery of whether fauna really existed at those depths.

(2) Commencement of Quantitative Surveys

After the voyage of the Galathea in 1951, the interest of deep sea biology changed from natural history surveys, with a focus on taxonomy, to quantitative surveys (Fujita, 1988). It is no overstatement to say that quantitative surveys developed together with developments in sampling equipment. A typical example of this is the replacement of grab samplers by core samplers, which greatly improved the sample quality.

In the Galathea survey, a Peterson grab, which was quantitative for that period, was used. Many samples were collected with it, which yielded a variety of macrobenthos and other benthic organisms from the Pacific Ocean. This survey also succeeded in sampling fauna from a depth of 10,200 m in the Philippine Trench, and confirmed the existence of fauna in the ultra-abyssal zone (Mill, 1983).

The Peterson grab used in that survey, in addition to the grab samplers of Campbell and Okean, were used as the standard type of quantitative samplers until the 1970s. However, these samplers were developed by improving and enlarging the samplers used in coastal surveys so had deficiencies as deep-sea samplers. Some of these deficiencies included unsuitable claw shapes on the top of the grab, cutting into the sediment in a non-uniform way; and the shock of hitting the bottom blew away the surface slurry and small benthos.

Corers were the next generation of sediment samplers. The first person to use the corer-type sampler for quantitative sampling of abyssal fauna was Reineck (1963). That (Reineck box-corer) corer was improved from a geological survey corer, so it was highly airtight, enabling it to sample surface slurry without any problems. However, the volume of sample was so small that it was unable to cope with quantitative sampling of macrobenthos which have a low living density, hence it did not come into wide-use. To overcome these problems, Hessler & Jumars developed the USNEL box corer in 1974. This corer penetrated the sediment with high precision; it covered an area of 0.25 cm^2 which is large enough to provide a meaningful number of organisms even at low population densities; and it provided samples with superior quantitativeness compared to conventional grab-type samplers (Smith & Howard, 1972). This corer is still the standard type for sampling macrobenthos today.

Research into meiobenthos and bacteria requires even more delicate sampling than macrobenthos. Thus the USNEL box corer was still inadequate for all deep-sea biologist's needs. This led to the development of the multiple corer developed by the Scottish Marine Biological Association (SMBA). This sampler only has a small impact when it hits the bottom, thus keeping the "blowing away" effect to a minimum and preventing the meiobenthos and bacteria distributed on the surface of the sediment from escaping. In an actual comparison of the sampling ability of the two corers, it was reported as being significantly superior in quantitative sampling of meiobenthos (Shirayama and Fukushima, 1995).

With regard to megabenthos, these fauna are too rare to be collected in numbers sufficient for quantitative estimation by sediment samplers such as a box corer. Trawling or dredging causes extensive damage to samples, which leads to problems with species identification. Therefore, no standard method for quantification of megabenthos has been established. At present, visual observation using video / still camera is considered to be the optimum method for quantitative observation. However there are many problems that still need to be overcome (Christiansen and Thiel, 1991).

(3) The Beginning of the Ecological Approach

Quantitative study of abyssal benthos is currently one of the most important research subjects in deep sea benthology, with new areas of study opening with the development of survey equipment that has enabled approaches from a variety of viewpoints. Thus studies that were not carried out previously, such as those in the field of physiology are now being undertaken.

The turning point for this change was an accident with a submersible. In 1968, the "Alvin" belonging to Woods Hole Oceanographic Institution, sank to the bottom to a depth of 1540 m, with its hatch still open. Inside the Alvin, salvaged after approximately ten and a half months, sandwiches and apples which remained had hardly decomposed at all. From this accident it became clear that the decomposition activity of abyssal microbes was markedly slow, and it spurred great interest to the study of deep sea microbiology at the time (Naganuma, 1997).

The latter half of 1960s saw a lot of survey equipment developed, and a variety of methods were applied in field surveys. The most revolutional was the manned submersible, which allowed direct observation of the deep sea. It became possible to see with one's own eyes the images of the abyssal bottom, which could formally only be glimpsed through sampling gear or which, were drawn in one's own imagination. It also became possible to carry out physiological experiments on the spot. The most notable result was the discovery of chemical compound community around the hydrothermal vent in Galapagos Bay by the New Alvin in 1977. In subsequent years, not only hydrothermal, but also hot and cold seep spots and their biotic communities were discovered using submarines. Submarine surveys continue to be carried out but since they provide data for variety of projects, and there are a limited number of submarines, there are limits to the frequency with which surveys can be carried out. Consequently, there is a tendency for the order of priority in survey objectives to be limited to those surveys that can only be carried out using submarine. Thus sediment samplers such as box corers or multiple corers are still generally used to carry out simple surveys, such as biomass estimation.

(4) Large Scale Surveys with Deep Sea Development

Deep Sea Biology is not limited to basic science. It also has aspects that have developed through links with industry. The most prominent examples are the environmental studies, which have accompanied mining surveys for manganese nodules.

Ball-shaped manganese nodules are a mining resource, which are found on the abyssal bottom throughout the world. The resource includes not only manganese oxides but also includes steal, copper and high grade rare metals such as nickel and cobalt.

Until recently, many countries that produced and supplied these rare metals were hindered by political instability and weak supply infrastructure, so there has been an increasingly strong push towards obtaining these resources from the ocean. From the 1960s, various countries commenced exploration of deep-sea resources, and from the 1970s commenced environmental research, which precedes deep-sea mining developments. The initial surveys represented by The Deep Ocean Mining Environmental Study (hereinafter DOMES) of America's National Oceanic & Atmospheric Administration (hereinafter NOAA) of the Department of Commerce focused on deep-sea properties including benthic fauna. From the late 1980s, in situ experimental studies were carried out and it became the main theme of deep-sea environmental studies. Specifically, these studies have been DISCOL (Disturbance and Recolonization Experiment in the Deep South Pacific Ocean: 1989 onwards) carried out by Germany, BIE (Benthic Impact Experiment: 1995 to 1995) carried out by the United States, JET (Japan Deep Sea Impact Experiment: 1995 to 1997), IOM' BIE (1996 onwards) carried out by IOM (Interoceanmetal), the joint organization of former Eastern Bloc Countries, INDEX (1996～) carried out by India, and Korea intends to implement a similar study from 1999.

These studies contrast to surveys in the past because they not only have a strong scientific base, but also have the clear objective of assessing deep-sea impacts from anthropogenic achieves. As national projects, they attracted a great amount of funds, if only temporary, who resulted in large-scale, comprehensive, studies being undertaken.

3. THE PRESENT STATE OF, AND PROBLEMS IN, DEEP SEA BIOLOGY

(1) Environmental factors

In the past, when the information about the deep sea environment was limited in time and space, it was described by adjectives such as calm, uniform and stable in addition to dark, high pressure and low temperature (Shirayama and Fukushima, 1997). This is why Sanders (1968) advocated the "Stability Time Hypothesis" to explain the diversity of deep-sea benthos.

The development of better survey gear provided interesting and new facts that changed our understanding of deep-sea biology. For example, deep sea areas in zones of high pelagic productivity, or those closer to shore, have a higher abundance of benthic organisms than other deep sea areas (Filatova, 1982, Khripounoff et al., 1980, Sibuet et al., 1984, Sibuet and Segonzac, 1985). Subsequent research studies were then undertaken to understand the mechanism controlling deep-sea biodiversity. Shirayama (1984) has studied benthos in both high and low productivity sites, and suggests that deep sea meiobenthos can be estimated by a three function formula, viz.: the quantity of flux from the pelagic zone (i.e.: food supply), the quantity of organic carbon on the bottom (food stock) and grain size (habitat). Thiel et al. (1989) proposed that seasonal changes in the input of organic matter to the deep sea bottom corresponds to the changes in pelagic productivity. They also noted that there are some organisms whose biomass adjusts in response to seasonal changes.

These studies exploded the former image of deep-sea ecosystem as a stable system and described it with higher precision. They showed that the deep-sea benthic community varies with changes in environmental factors. However there is still much to learn before we fully understand the deep-sea benthic communities.

To be exact, we need to substantiate these relationships, the results must be verified after possible effects of other factors have been ruled out, and the causes of variation must be determined.

(2) Quantitative Survey Problems

In ecological studies, it is important to quantify the abundance and biomass of the community being studied. It is necessary to evaluate those data objectively and compare them with similar data from other sites. In this case, the data to be compared should be treated in the same manner. It is also important that the data are comprised of a statistically adequate number of samples and expressed as representative profiles of the respective site.

In the field of deep-sea biology, however, it is rare that these conditions can be met. Therefore objective evaluation is often difficult as exemplified by the Pacific Ocean; there have only been a few deep-sea biological surveys. In the following section then, the case where problems of estimation of meiobenthic abundance, macrobenthic abundance and megabenthic abundance are described.

a. Meiobenthos

The history of meiobenthology is very short. It was only 50 years ago when fauna smaller than macrobenthos were given the name "meiobenthos" (Mare, 1942), and it was even later than that the field of study extended to the deep sea.

Before 1970, only two quantitative studies had been undertaken on deep sea meiobenthos: one was carried out a continental shelf off the coast of Massachusetts (Wilgley and McIntyre, 1964) and another in the deep sea off eastern Africa (Thiel, 1966). After these studies, deep-sea research increased gradually, but most was conducted in the Atlantic Ocean. In the Pacific Ocean, excluding studies on hydrothermal vents and cold seep, only four studies by Thiel (1975), Snider et al. (1984), Renaud-Mornant and Gourbauld (1990), and Shirayama (1984), had been made before 1991 (Tietjen, 1991). Furthermore, a box corer of the old standard-type was the sampling gear used in these studies. Thiel and Schriever (1989, 1990) was the first person to report meiobenthic abundance using a multiple corer in the Pacific Ocean.

b. Macrobenthos

In macrobenthos studies, similar to meiobenthos studies, the standard sampling "grab sampler" was replaced by the box corer around 1974 (see Part 1). However this change occurred much earlier than the meiobenthos case so there are many more macrobenthos data sets. This does not mean that macrobenthic quantitative studies are without problems. One of the most serious problems is that different researchers inconsistently classify the fauna into different size categories, so it is difficult to compare abundance between studies. Representative sizes are 0.5 mm (Frankenberg and Menzies, 1968), 0.42 mm (Carely, 1981, Hecker and Paul, 1979; Rowe et al. 1982), 0.297 mm (Smith, 1978; Jumars and Hessler, 1976, Hessler and Jumars, 1974) and 0.12 mm (Paul and Menzies, 1974; Rowe, 1983).

Smith (1978) compared his data using 0.297 mm sieve with the data of Sanders et al (1965) who used a 0.42 mm sieve in the same area, and he pointed out his estimated abundance was more than that of Sanders et al. Jumars and

Hessler (1976) concluded that 15% of the individuals are lost from using 420 mm rather than 297 mm sieve.

Many deep-sea macrobenthos biologists are well aware of size category problems. Therefore it was proposed at the International Sixth Deep-Sea Symposium to standardize macrobenthos size categories (Shirayama, 1992).

c. Megabenthos

It is true that our knowledge about the abundance of meio- and macrobenthos in the deep sea are quite limited, but it is much better than our knowledge of the megabenthos. This is because megabenthos biomass data are scarce due to logistical sampling problems. Currently there is no established method to estimate the abundance of these fauna which have a much larger size, lower density, and are quick movers (Christiansen and Thiel, 1991).

Currently, quantitative estimates can only be made by seabed video observations, but we should bear in mind that only part of the megafauna is detected such that: only specimens exceeding a certain size can be identified; infaunal organisms usually are not recognized; and large motile animals may avoid the camera vehicle (Christiansen and Thiel, 1991).

This kind of research is mainly conducted on continental shelves and in the bathyal zone (Rice et al. 1982; Haedrich and Rowe, 1977; Lampitt et al., 1986; Grassle et al., 1975), with only limited research in the abyssal zone. To the best of this author's knowledge, examples of abyssal zone research in the North Pacific are Foell (1992), Foell et al. (1986), Hecker and Paul (1979), Pawson and Foell (1983), and Morgan et al. (1993). These studies, except for Morgan et al. (1993), were all USA Government reports.

d. Faunal Composition Study Inconsistencies

As described above, there are few data available to estimate the abundance of each faunal group, such that data covering the total size range of meio-, macro- and megabenthos are quite rare. Snider et al. (1984) assessed the biomass and abundance of nanobiota, meiofauna and macrofauna, but did not include megafauna. In more recent studies, the DISCOL program researched meio-, macro- and megabenthos, the BIE program assessed macro- and meiobenthos, and the IOM BIE studied meio- and megabenthos.

Although our knowledge of deep-sea fauna extends over only one century, deep-sea biology is developing with a variety of factors including better taxonomy and quantitative surveys using an ecological approach. These studies cover large areas and overlap in time among survey areas. In other words, deep-sea biology has diversified since the 1950s to such an extent that it is now impossible to review it without classifying it into a variety of sections. It is expected that the field of deep-sea biology will continue to be approached from these perspectives in future.

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