



Title	COMMUNITY STRUCTURES OF THE MACRO-BENTHOS IN THE SHALLOW WATERS IN NORTHERN JAPAN
Author(s)	NAKAO, Shigeru
Citation	MEMOIRS OF THE FACULTY OF FISHERIES HOKKAIDO UNIVERSITY, 28(2), 225-304
Issue Date	1982-03
Doc URL	http://hdl.handle.net/2115/21872
Type	bulletin (article)
File Information	28(2)_P225-304.pdf



[Instructions for use](#)

COMMUNITY STRUCTURES OF THE MACRO-BENTHOS IN THE SHALLOW WATERS IN NORTHERN JAPAN*

Shigeru NAKAO

Faculty of Fisheries, Hokkaido University, Hakodate, Japan

Contents

	Page
I. Introduction	226
II. Materials and methods	228
1. General description of the areas investigated	228
2. Sampling methods of benthos	231
3. Analytical methods of sediment and water for the measurement of the physical and chemical environment	232
III. Environmental characters in the fields investigated	233
1. Sedimentary environment	234
(1) Zyusan-ko	234
(2) Notoro-ko	235
(3) Hakodate Bay	236
2. Water environment	237
(1) Zyusan-ko	237
(2) Notoro-ko	241
(3) Hakodate Bay	245
3. Discussion	245
IV. Structure of benthic communities	246
1. Species compositions and the distributions of dominant species in time and space	246
(1) Zyusan-ko	246
(2) Notoro-ko	247
(3) Hakodate Bay	250
2. Community types and their distributions in time and space	255
(1) Zyusan-ko	257
(2) Notoro-ko	261
(3) Hakodate Bay	265
3. Species diversities of benthic communities and changes in their seasonal distributions	269
(1) Zyusan-ko	270
(2) Notoro-ko	271
(3) Hakodate Bay	272
4. Discussion	273
V. Relationships between benthic communities and environmental factors	277
1. Community types and environmental factors	278
(1) Hakodate Bay	278
(2) Zyusan-ko	282
(3) Notoro-ko	283

* This work was submitted as a partial fulfillment of the requirements for Doctor's degree in Fisheries Science at Hokkaido University in 1980.

2. Species diversities and environmental factors	285
(1) Hakodate Bay.....	286
(2) Zyusan-ko.....	286
(3) Notoro-ko.....	287
3. Discussion	288
VI. Experimental application of the benthic community to the evaluation of shellfish bed.	289
1. Communities in the shellfish beds.....	290
(1) Ezo giant scallop beds	290
(2) Freshwater clam beds	291
(3) Surf clam beds	293
2. Discussion	296
VII. Summary	296
References	298

I. Introduction

Because of environmental complexity in the habitat, benthos in the shallow waters show various living manners, though all of them occupy a position at or near the end of a food chain items in marine ecosystems. Benthos must play an important role in the recycle or regeneration of nutrients between pelagic and benthic devisions, that is, without such larger animals as megalo-benthos they form an important source of the demersal fishes which work an indispensable role in trophic levels and also provide food directly or indirectly through the detritus food chains for various micro consumers in a lower trophic level. Thus, benthos with a role of this kind have a certain domain as a habitat according to their proper manners and form a community in which certain species will occur together in a prescribed areas.

An allusion to the benthic community concept can be found in the statement of Möbius (1877) on the community of organisms in an oyster reef as a "biocoenosis". Then the concepts of benthic community were expanded by Petersen (1913, 1918), Mollander (1930) and Thorson (1955a, 1957). They suggested that a community is any assemblages of species and individuals, as an organized unit that species composition and their frequency show regular changes in time and space, and that these numerical components keep a certain balance through a definite interspecific food relationship.

From these view points of a benthic community concept, the community can also be recognized as a statistical unit of real existence, for the community can be statistically measured on the basis of such data obtained until now as the spatial distribution of species and abundance of these individuals.

In this way described above, the types of community structure may be classified by means of mathematical techniques. With the advance of quantitative analysis approach of benthic community recognition recently it has gradually become clear that unique attributes of the benthic community type correspond to characteristics of bottom topography, sediment and water in the habitat (Yamamoto, 1950, 1955; Sanders, 1960, 1968; Kitamori, 1963; Horikoshi, 1962, 1970; Day et al., 1972).

From the fact mentioned above, we may consider that clarifications of the distributive and quantitative changes of the benthic communities in space and

time, and of response of the benthic communities to environmental conditions in the gradient will give not only important clues to the study of the characteristics of the organic matter flow in the bottom area, but also a fundamental knowledge to judge the habitat by fitness and to enlarge the habitat area of useful shellfishes found in the benthic communities through clarification of the environmental conditions of their physical habitat.

The benthic communities are largely changeable in the structure through reproduction and immigration of populations according to time and space (Yamamoto, 1952; Tanita and Okuda, 1956; Kikuchi, 1969; Holland and Polgar, 1976; Holland et al., 1977; Frankenberg and Leiper, 1977; Nakao, 1979). However, in spite of this, the studies on distributive structure and quantitative changes of benthic communities have been concentrated upon the seasonal quantitative changes of a particular species (Crocker, 1967; Ward, 1973, 1975) and of dominants (Kitamori, 1963; Kosaka et al., 1972; Holland and Polgar, 1976; Nakao, 1976; Frankenberg and Leiper, 1977) and also upon the community structure in a certain seasons (Yamamoto, 1951, 1954; Wigley and McIntyre, 1964; Kikuchi and Kikuchi, 1967; Kosaka et al., 1971; Hayashi, 1978). Therefore, as pointed out by Frankenberg and Leiper (1977), after clarification of temporal and spatial changes in component populations of communities and in environmental conditions in their habitats, and of relationships between them, the studies of the structural changes of the whole community are just a few now. Thus many of this field is still remained.

Therefore, the structural characteristics of benthic communities in relation to temporal and spatial changes in the shallow waters must be investigated in order to understand exactly the organic matter flow in the regions and to apply them to indicators of environmental gradients in the habitat. From this view, the present author has tried to clarify the characteristics of benthic structure in time and space, and correlation between them and environmental gradients in open and enclosed shallow waters around Hokkaido.

Here we have observed the environmental gradients of bottom sediment and water on the basis of physical and chemical analyses and species composition and dominant species in benthic communities in the surveyed areas. Secondly, community types have been classified by means of mathematical analysis and species diversity indices in each community type have been analyzed by statistical treatment, and data on benthic communities have been correlated with informations on their habitats described above. Finally, universal classifications of benthic communities occurring in the shellfish beds based on structural features have been examined and the possibility to estimate the shellfish beds on this basis have been attempted. Results obtained do not have the roles of the environmental factors in regulating community structure and the functional attributes of benthic communities. In this connections we cannot but acknowledge that the entire role of benthic communities in a benthic division have not yet been made clear.

To summarize our interpretation of the results obtained, we can explain the community types, their spatial and temporal distributions, relationships between structural community characteristics and environmental factors, parallel bottom

communities in the different geographic beds of the same shellfish, and efficiency of structural characteristics of parallel bottom communities as indicators in judging shellfish beds.

In preparing this presentation, the author is much indebted to Prof. Akira Fuji of the Faculty of Fisheries, Hokkaido University, for his untiring guidance and encouragement during the investigation and critical reading of the manuscript. He also wishes to express his thanks to Prof. Takao Igarashi, Prof. Kenichiro Kyushin and to Prof. Seikichi Mishima of the same university, for their helpful guidance and criticism in regard to the problems discussed in this paper.

Heartly thanks is expressed to Dr. Hikoei Ohmi, ex-professor of Hokkaido University, for polishing the English manuscript.

The author is indebted to the following taxonomists who gave guidance in the identification of samples, Dr. Minoru Imajima of National Science Museum, Prof. Tadashige Habe of Tokai University, Mr. Seiichi Irimura of Yokohama High School, Mr. Norizumi Kitagawa of Mie Scientific Educational Center, Mr. Noboru Nunomura of Toyama Science Museum, Prof. Yuki-yoshi Kamihira of Hakodate College.

Thanks are also due to Mr. Kazuo Kikuchi of the Hokkaido Abashiri Fisheries Experimental Station, Mr. Toshiaki Iwaki of the Faculty of Fisheries, Mie University and to Mr. Akihiko Kudo of the Hakodate City Office for their advice and patient help in field work.

II. Materials and Methods

1. *General description of the areas investigated*

Areas investigated in this study may be conveniently classified into two groups according to topographical features. One is the shallow embayment such as Zyusan-ko, Furen-ko, Notoro-ko and Saroma-ko, and the other is the open shallow water such as Hakodate Bay, Ishikari Bay, and the coastal areas along Tomakomai and Hachinohe. Localities and topographical outlines of these areas described above are shown in Figs. 1 and 2.

Lagoon Zyusan-ko: this lagoon is a small mixohaline lake situated at the west side of Tsugaru Peninsula in northwestern Aomori Prefecture with about 18 km² in area. Iwaki River and its branches flow into the lagoon in the south-eastern side and in the northwestern side, the narrow opening of the lagoon is connected with Japan Sea through the short waterway. About 60% of the area has a water depth shallower than 1 m. The action of tides against the flow of the rivers produces a very complex mixture of salinities and except the area near the opening the surface water is frozen in winter from December to March showing low salinity. The lagoon is well known as one of the good fresh water clam beds of which only a few are found in Japan, as Lake Shinji-ko and Lagoon Hachiro-gata. The clams are caught in large quantities ranging from 2,000-3,000 tons per year in the lagoon.

Lagoon Furen-ko: this lagoon enclosed by the developmental sand bar is situated face to face with Nemuro Bay and is about 53 km² in area. It has two parts in salinities, one is outer area higher in salinities, with sea water penetrating

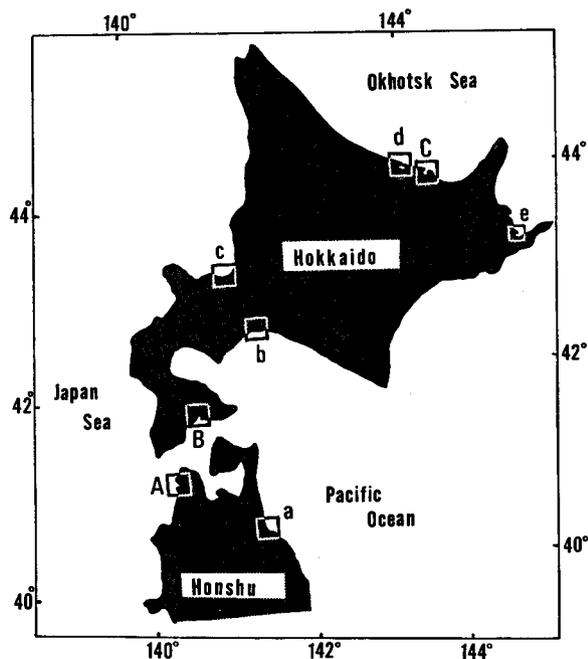


Fig. 1. Investigated areas adjacent to North Japan.

A: Lagoon Zyusan-ko, B: Hakodate Bay, C: Lake Notoro-ko, a: Coast along Hachinohe, b: Coast along Tomakomai, c: Ishikari Bay, d: Lake Saroma-ko, e: Lagoon Furen-ko

from the opening, and the other lower, with fresh water inflow from major three rivers. It does not show, however, distinct changes in seasonal distributions of salinity because of the larger rate of penetration of sea water as compared with that of the inflow of fresh water. The clams are caught 100 tons in quantities per year in the inner part shallower than 1 m depth.

Lake Notoro-ko and Lake Saroma-ko: these lakes which are situated on the coast along Okhotsk Sea are mixo-polyhaline lakes and both are well known as good scallop beds.

Formerly the opening of Lake Notoro-ko had become narrower and shallower by an accumulation of sand from late autumn to early spring, and during these four months both the outflow of the lake water and the inflow from the Okhotsk Sea water outside had been prevented. In April 1974, the opening was artificially constructed to dredging and was thus enlarged. Hence the amount of both the inflow and the outflow increased remarkably not only in the cold seasons but also in the other seasons. Lake Notoro-ko is in the midst of a changeable process from the disharmonic bay to the harmonic bay and benthic communities observed in it are noticeable in successional changes in structure. On the other hand, Lake Saroma-ko is a homoiohaline in response to a large quantity of sea water interchange.

Hakodate Bay: it has the shape of a half circle, with a wide opening of ca. 8 km

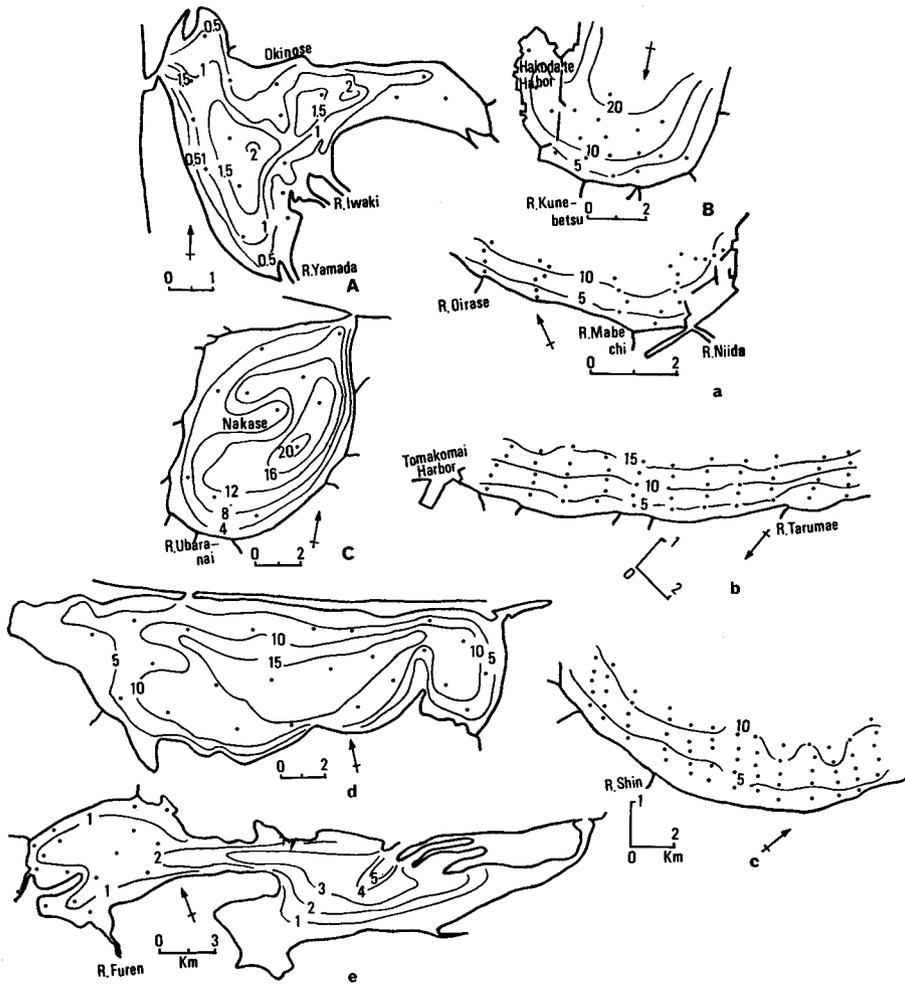


Fig. 2. Map showing the situations of the sampling stations and water depth (m) in the investigated areas. See Fig. 1 for A-e.

and it has a topographical similarity to an open coast. Hakodate Harbor is located in the inner part and the four rivers flow into the bay. It forms two different shellfish beds, one is a surf clam bed in the inner part and the other, a scallop bed in the central part.

Coastal areas along Hachinohe, Tomakomai and Ishikari Bay: all these areas are open coasts with sandy beaches behind and have surf clam beds. In Hachinohe, the harbor was constructed in the shallow area between Mabechi and Oirase estuaries in 1966. Hence it appears that a change of tidal current and an increase of organic pollution have influenced the benthic community structure of the surf clam bed.

2. Sampling methods of benthos

For quantitative studies, both the mesh size of the sieve and the benthos sampler used are of critical importance in determining the size range of the animals to be collected. Animals separated from the sediment can differ considerably in species and individuals according to the mesh size used (Mistakides, 1951; Holme, 1953; Hartman, 1955; Reish, 1959). On the other hand, benthic animals can be recognized as a series in size and divided into the three arbitrary divisions, macro, meio, and microbenthos (Mare, 1942; McIntyre, 1969; Huling and Gray, 1971). Because different techniques are required for each group at both the sampling and the separating stages, we should define initially the size range of animals to be collected for statistical conclusion in numbers of species and of individuals.

Animals studied in the present paper are macrofauna for which 1 mm sieve, in general, is used for collection, therefore meio and microfauna which can pass through this sieve are not treated. As described already, since the size of animals to be collected is defined we need not consider the problems of the mesh size that arise mainly at the sieving stage.

For sampling the macrofauna, Tamura grab (Tamura, 1953) covering a surface area of 1/17 m² was commonly used on sandy and muddy shores. In coarser sediment such as Zyusan-ko, a coring device covering a surface area of 177 cm² was employed. To test how many sampler hauls are sufficient to collect a high proportion of the species and the individuals, the recruitments of species and individuals to the sample total from each successive haul by plotting on a cumulative basis the number of species and of individuals respectively against the number of hauls are examined at two stations with different particle composition (Table 1 and Fig. 3). As shown in Fig. 3, species or individuals/area cumulative curves indicate that five replicate samples at least are required to give an acceptable estimate of the number of species and of individuals respectively. Then five samples were collected at each station in the surveyed areas. The samples found on the 1.0 mm mesh were sorted at the higher taxa level and, when possible, to the species level under a dissecting scope and total per square meter were then calculated.

Table 1. Particle compositions of the muddy and the sandy bottoms comparing the sampling efficiency of two samplers.

Particle size (φ)	Particle composition %	
	Muddy bottom	Sandy bottom
-1>	0.3	4.0
-1~0	0.8	3.1
0~1	1.3	5.6
1~2	7.5	10.8
2~3	15.3	26.2
3~4	26.3	21.6
4~5	26.3	13.5
5~8	14.3	8.6
8<	7.9	6.6
Water depth (m)	4.5	0.5

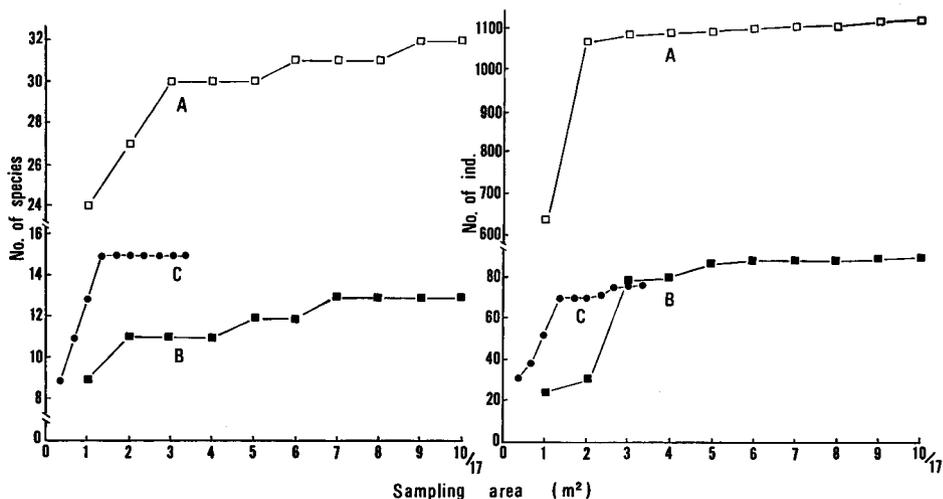


Fig. 3. Cumulative plots of species (left) and of individuals (right) taken in successive samples. A: Tamura grab sampler at the muddy bottom. B: Tamura grab sampler at the sandy bottom. C: Core sampler used at the sandy bottom.

3. Analytical methods of sediment and water for the measurement of the physical and chemical environment

A small amount of surface sediment in 2 cm obtained from the same grab sample as used in the collection of fauna was stored on the polyethylene bottle and frozen as soon as possible to prevent organic matter decomposition caused by micro-organisms.

It was taken to the laboratory and after being melted and adequately prepared previously, the following examinations have been carried out. The methods used for these examinations were as follows.

1. Total carbon content was determined using a Yanagimoto C-N corder MT 500 instrument.
2. Total nitrogen content as also determined using the same as the above.
3. Total sulfide content was determined by Tomiyama and Kanzaki method.
4. Particle composition was determined using a sieve series and a Hitachi PSA 2 instrument.

Total carbon, total nitrogen and total sulfide contents were estimated in percentage weight of the sediment, and particle composition was measured in percentage weight of each size fraction in the total weight of sediment. Sediment can be characterized with respect to its percentage content of three variables, for instance, fractions of a size smaller than 2.50ϕ in grain size diameter, ranging from 2.50 to 3.25ϕ and larger than 3.25ϕ , and a sand type was represented according to sand type diagram method (Sato, 1959) with respect to the percentage content of three variables.

Water samples were taken by Kitahara B type sampler, and bottom water samples of ca. 2 cm off the bottom were taken using the instrument which the injector of 25 cc in capacity was fixed to the plain plate.

Interstitial water for chlorinity analysis was extracted from the 2 cm surface sediment of the bottom by using a centrifuge.

Objects and methods of water analyses were as follows.

1. Dissolved oxygen content was determined with a Winkler method.
2. Chlorinity was determined with a Fajans method.

III. Environmental characters in the fields investigated

It is well known that the relationships between certain environmental variables and the distribution of benthic macrofaunal elements have been virtually existed (Petersen, 1913; Blegvad, 1930; Miyadi, 1938, 1940 a, b, c; Yamamoto, 1950, 1955; Sanders, 1960, 1968; Horikoshi, 1962, 1970; Kitamori, 1963), and the relationships can be considered to arise reasonably with three biological meanings as follows; (1) response to variable substrata according to benthos behavior, for instance, creeping, burrowing, and attaching, (2) nutritional factor given in the quantity of food supply to benthos in edible forms required (3) tolerable ability of benthos to environmental limiting factors. Since benthic animals in sandy and muddy shores show a direct dependence on the particle composition of the sediment as a convenient support (Davis, 1925; Thorson, 1955a; Sanders, 1960, 1968; Horikoshi, 1962, 1970), it was determined in connection with (1). Contents of organic matter in the sediment related to the distribution of organisms (Petersen, 1913; Jensen, 1919; Blegvad, 1928; Bader, 1954), carbon and nitrogen contents, therefore, were measured as an indicator of organic matter content in connection with (2). In connection with (3), benthic animals are markedly influenced in terms of physiological tolerance by salinity (Beadle, 1937; Gunter, 1945; Smith, 1955 a, b; Fuji, 1957; Yamamoto, 1959; Welis, 1961; Remane and Schlipfer, 1971), oxygen deficiency (Miyadi et al., 1950; Rosenberg, 1973) and sulfide content (Yoshimura and Wada, 1938; Miyadi, 1938, 1940 a, b, c; Seisi and Tomiyama, 1942; Miyadi et al., 1944; Theede et al., 1969), these three environmental factors, therefore, were determined in relation to water or sediment.

The characteristics of environment in areas investigated were subjected to examinations of three environmental sides described above.

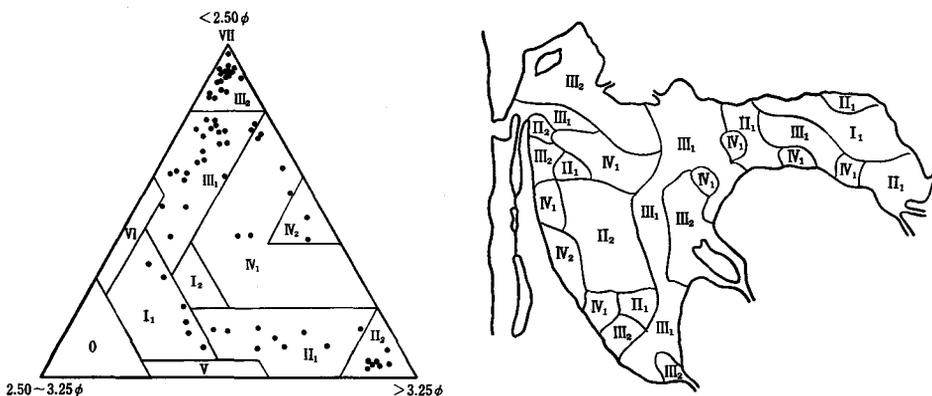


Fig. 4. Sand types divided by means of sand type diagram method (Sato, 1959) (left) and their horizontal distribution (right) in Lagoon Zyusan-ko.

1. *Sedimentary environment*

(1) Zyusan-ko

Horizontal distribution in sand types obtained by using a Sato method is shown in Fig. 4. It shows that sand types very well sorted are not found and type II₁, well sorted very fine sand, and type II₁, commonly sorted very fine to fine sand are distributed in the deeper area from the opening to the Yamada River estuary. Type IV, ill or very ill sorted sand found in neighboring areas, will be attributed to the mixture of depositional fine materials transported by the rivers and coarse sand resuspended by wave action. The eastern area in the lagoon is occupied by sand types of I₁ and I₂ predominated by fine sand and II₁. In the shore shallower than 1 m depth, sand types of III₁, commonly sorted median to fine sand and III₂, coarse sand spread. In general, the distribution of sand types in Zyusan-ko, particle compositions in between areas shallower than 1 m and central part deeper show a difference, namely, from the shallow area toward the central part, the sand types show the distributive change such as III₂+III₁→IV→II₁+I₂, and the difference in quality of sediment results to be smaller in particle size continuously from the shore to the center of the lagoon with an increasing water depth.

Areal distributions of total carbon, total nitrogen and total sulfide contents in sediment (Fig. 5) are extremely similar to one another in time and space. These values are comparatively high in the central part and decrease gradually toward the

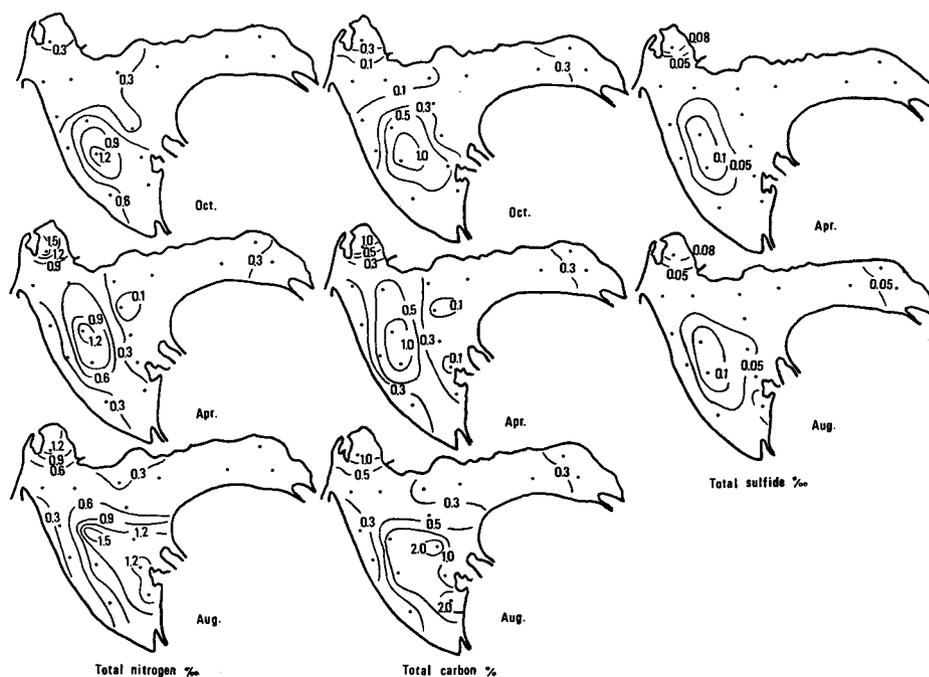


Fig. 5. Map showing the chemical characteristics of the sediment in Lagoon Zyusan-ko.

Table 2. Particle composition (%), Md (ϕ) and sand type of the sediment in Lake Notoroko in 1972 before (upper) and after (under) the mouth was artificially constructed.

	St.	Depth m	Particle size (ϕ)							Md (ϕ)	Sand type
			-1>	1~0	0~1	1~2	2~3	3~4	4<		
1972 Summer	1	8.5	1.1	2.0	4.9	22.4	42.5	13.0	14.4	2.4	III ₁
	2	10.5	0	0.3	1.9	24.1	33.9	16.1	23.7	2.7	III ₁
	3	8.0	0.8	1.0	3.0	20.5	43.9	16.2	14.2	2.5	III ₁
	4	14.5	0	0.2	1.5	24.5	20.0	13.8	39.0	3.2	VI ₁
	5	8.0	0	0.6	3.8	42.2	45.1	4.8	3.5	2.5	III ₁
	6	6.4	0.2	0.5	13.7	31.2	30.2	11.0	13.2	2.2	III ₁
	7	16.0	0	0.3	2.2	21.3	18.0	15.1	43.1	3.5	VI ₁
	8	8.5	0.2	0.5	1.9	7.4	53.9	19.0	17.1	2.7	III ₁
	9	19.0	0	0.1	1.1	31.0	19.3	12.3	36.2	3.0	II ₁
	10	18.0	0.3	0.3	3.0	27.5	21.8	13.5	33.6	2.9	II ₁
	11	7.0	1.1	1.0	1.0	9.0	42.2	34.5	11.2	2.9	VI ₁
1978 Summer	1	10.0	0.7	1.0	6.2	37.5	30.0	4.0	20.6	2.1	VI ₁
	2	6.5	0.1	3.0	14.0	37.0	16.0	2.0	27.9	1.9	III ₁
	3	7.5	0.1	1.0	11.0	36.0	25.0	3.0	23.9	2.2	III ₁
	4	14.5	0	1.0	5.0	26.5	20.0	10.0	37.5	3.7	VI ₁
	5	7.5	1.0	11.0	25.0	31.0	15.0	1.0	16.0	1.3	III ₁
	6	6.0	2.0	2.5	11.1	28.0	36.0	8.5	11.9	2.2	III ₁
	7	17.0	0.1	0.8	1.0	10.0	28.0	29.5	30.6	3.4	VI ₂
	9	19.0	0.5	1.0	2.0	9.0	29.0	25.5	33.0	3.3	VI ₁
	10	21.0	0.2	0.5	1.0	5.0	39.0	33.0	21.3	3.2	II ₁
	11	8.0	0.1	0.7	0.9	4.5	36.0	41.0	16.8	3.1	VI ₁

shore. In connection with these distributions in space, particle components become smaller with the increasing of water depth.

In summary, it will be demonstrated on the sedimentary environment of the lagoon that seasonal variations of particle composition and contents of chemical components in sediment are only small and that the distributions of carbon and nitrogen contents which can be used as indicators of organic matter content are similar in time and space with each other.

(2) Notoro-ko

Results of particle size analyses in 1972, two years before and in 1978, four years after the construction of an artificial opening are shown in Table 2. In both two years, very fine sand fraction predominates at the stations (4, 7, 9 and 10) situated in the deeper central part and fine sand fraction at most stations in shallower waters. Near the shore and "Nakase" in central part with a comparatively shallower depth are found to contain sand types of III₁, ill sorted fine to coarse sand. The deeper area is occupied by sand type of IV₁, ill sorted sand and the deepest central area by sand type of II₁, commonly sorted very fine to fine sand. It can be said that there is little difference in particle compositions before and after the construction of this opening. As is evident from Fig. 6 showing areal distributions of contents of total carbon, total nitrogen and total sulfide in sediments collected in 1972 and 1978, they are very similar to each other in time

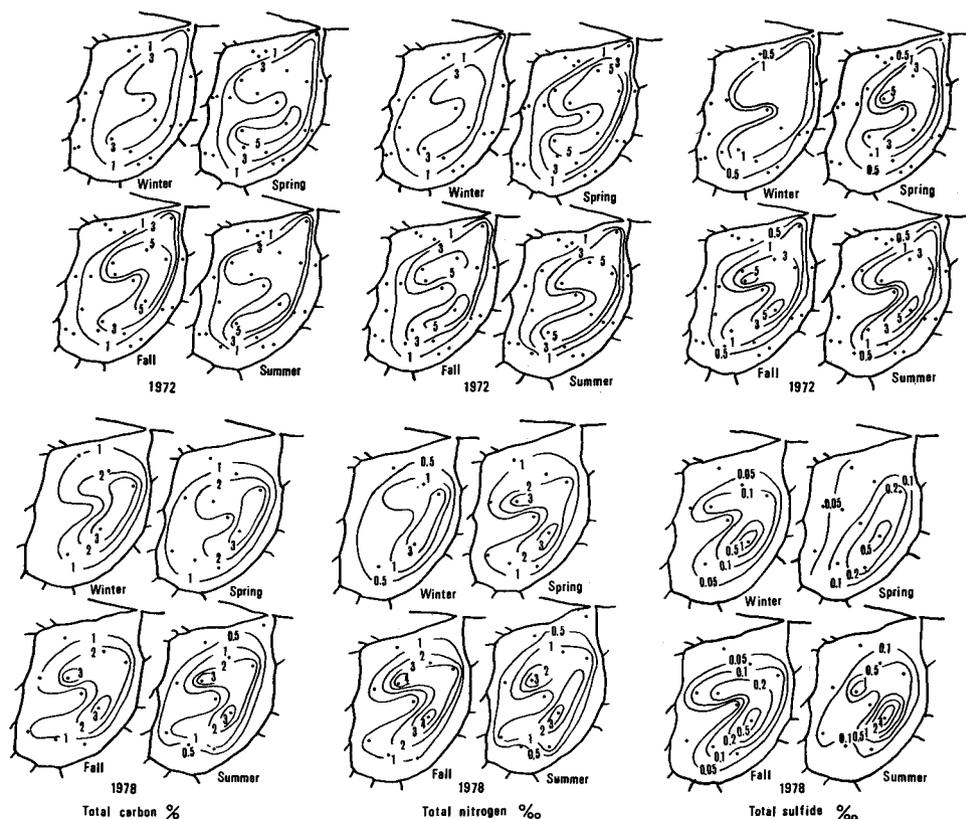


Fig. 6. Seasonal distributions of the chemical components of the sediment in Lake Notoro before (upper) and after (under) the mouth was artificially constructed.

and space. Namely the bottom sediments in the lake show an increase in these contents with an increase in water depth in both years. Their values in 1978, however, become remarkably lower than those in 1972, especially in the deeper area. The relation between carbon contents and water depth, therefore, is shown in Fig. 7 obtained from results before and after the construction of the opening. In 1972 carbon contents increase discontinuously with an increasing depth and suddenly at the deeper stations than ca. 12 m in depth. In 1978 these values increase gradually with an increasing depth.

The sulfide content shows smaller than 0.5 ‰, near the shore, and higher than 5 ‰ in the central deepest area in 1972. On the contrary, the value in 1978 shows lower than 1 ‰ in the whole areas except the central part showing 4 ‰ in summer.

(3) Hakodate Bay

Sand types characterized in relation to percentage of three variables are shown in Fig. 8. Hakodate Harbor and the central part of Hakodate Bay are occupied

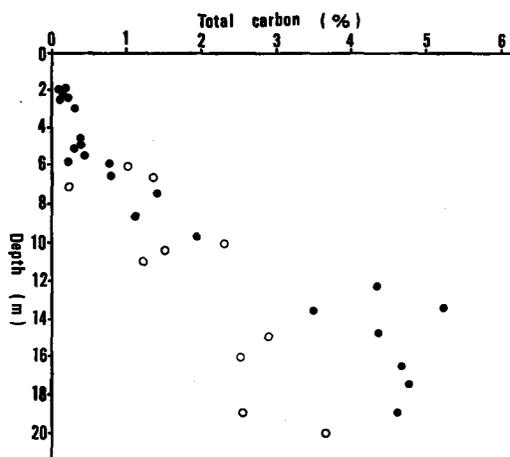


Fig. 7. Relationship between total carbon content in the surface sediment and the water depth in Lake Notoro-ko. Solid circles show the samples in Augusts 1972 and 1973 and open circles indicate the samples in August 1978.

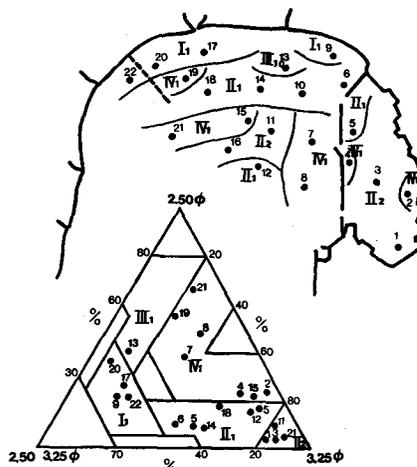


Fig. 8. Distribution of sand types divided by means of sand type diagram method in Hakodate Bay.

by the sand type of II_2 , well sorted very fine sand, and the inner parts are found to contain the sand types of II_1 , commonly sorted very fine to fine sand and I_1 , well sorted fine sand. While, the outer parts are occupied by the sand types of IV_1 , ill sorted sand and II_1 .

Seasonal distributions of carbon and nitrogen contents in sediment are similar in time and space to each other, and the seasonal variations are only small (Fig. 9), that is to say, comparatively high values are seen in the central part and Hakodate Harbor and centering around the central parts their values decrease gradually toward the shore and the opening of the bay. The sediment in Hakodate Bay is characterized as mentioned above in that the finer particles of clay or mud with quantities of minute organic remains are not deposited on the coast where there is wave action but are deposited in the central deeper water and Hakodate Harbor, where there is a weak turbulence. On the contrary, in the outer deepest water, fine particles are not deposited where the counterclockwise current is active and rather strong on the bottom (Hakodate Development Construction Office, 1979).

2. Water environment

(1) Zyusan-ko

Sectional distributions of chlorinity in water from the opening of the lagoon to the inflow of the Iwaki River are shown in Fig. 10. As understood from it, chlorinities lower than 1.0 ‰ are distributed in the water from the surface to 1 m depth layer, and the seasonal variations are only small, whereas, in water deeper than 1.5 m, chlorinities higher than 15 ‰ in summer are changed by those lower

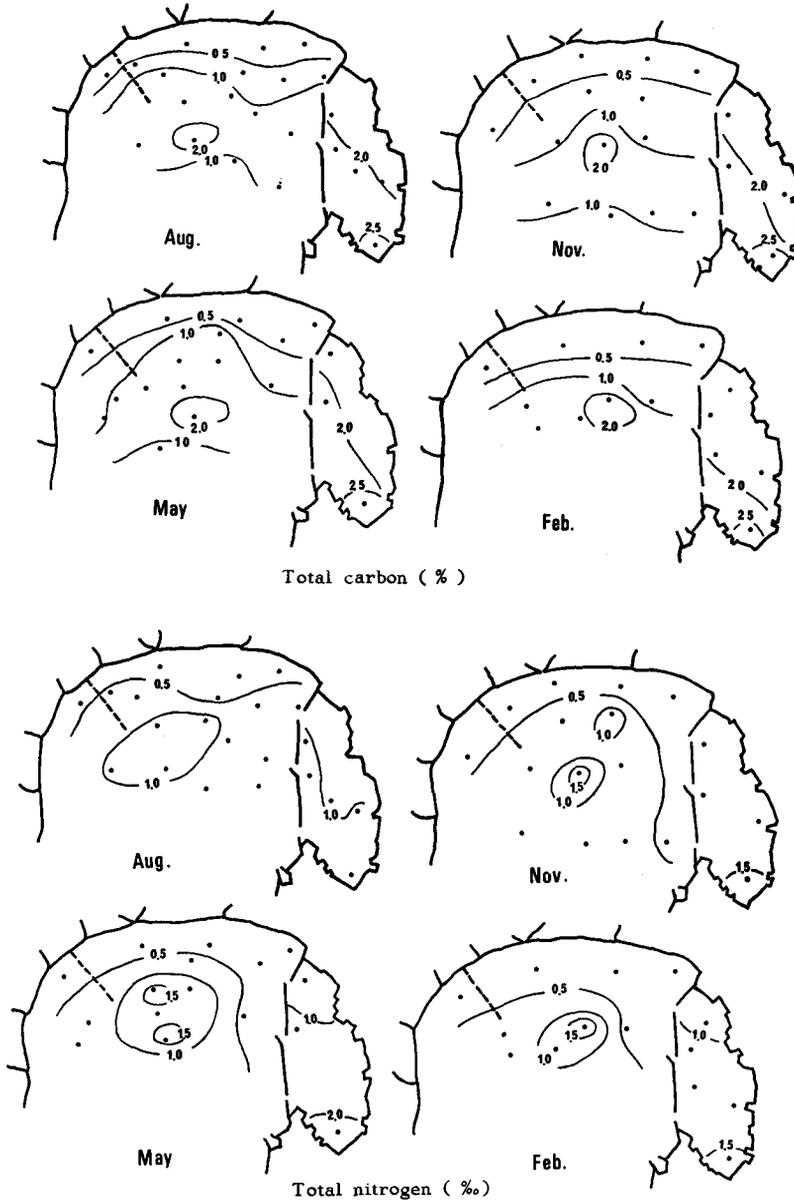


Fig. 9. Seasonal distributions of total carbon (%) (upper) and total nitrogen contents (‰) (under) in the surface sediment in Hokodate Bay.

than 5 ‰ from fall to spring. Such seasonal variations in chlorinity as seen in deeper water than 1.5 m depth are also clearly recognized as shown in Fig. 11. It shows the horizontal distribution in chlorinities in bottom water 2 cm off the

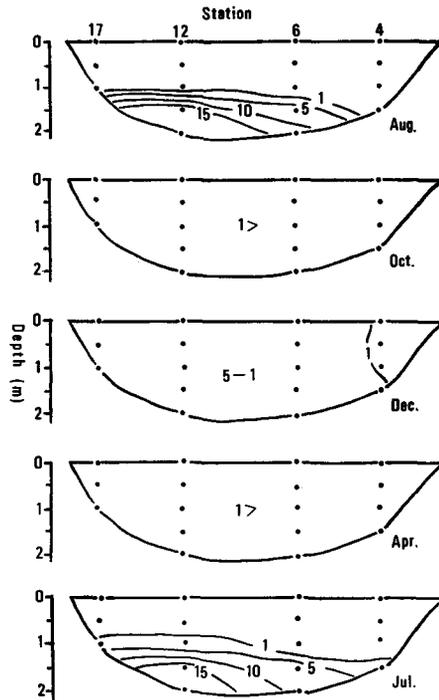


Fig. 10. Seasonal changes in the vertical distributions of chlorinity (‰-Cl) in the area from the mouth (St. 17) to the estuary of the Iwaki River (St. 4) in Lagoon Zyusan-ko.

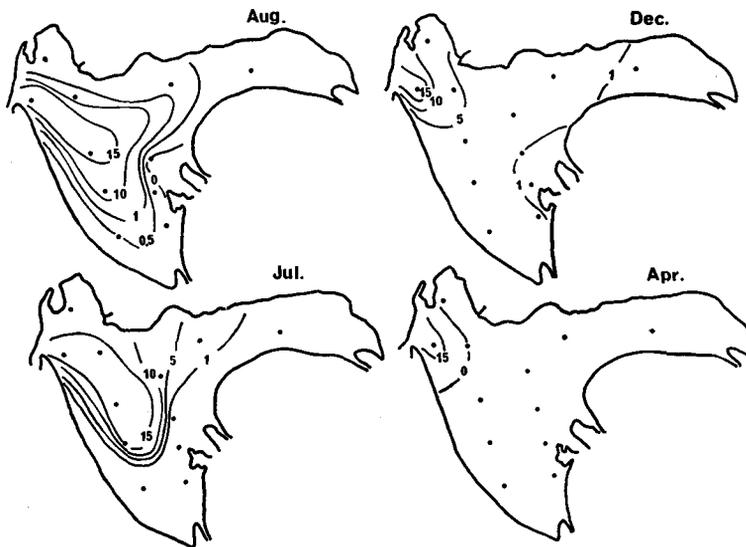


Fig. 11. Seasonal changes in the horizontal distributions of chlorinity (‰-Cl) in bottom water in Lagoon Zyusan-ko.

bottom. In short, the variations in chlorinities in the bottom water are widespread, ranging from higher than 15 ‰ in the opening of the lagoon to zero ‰ in the inner part (Fig. 11). In the warmer seasons, the chlorinities show higher than 15 ‰, spreading out from the opening to the central regions of the lagoon, and the values are found to be less than 1 ‰ in the inner parts. In winter and spring, values more than 15 ‰ are found in the extremely limited area around the opening, and other greater parts are occupied with low chlorinities less than 5 ‰ in winter and with fresh water in spring. It may be said that there is often an accompanying vertical gradient as described above, with the lighter fresh water flowing in at the surface and the heavier sea water flowing in beneath, and its seasonal variations vary in space and content with the quantity of flowing fresh water and tide. The chlorinities of interstitial water, however, do not show seasonably such evident variations as those of bottom water but show a similar distribution to each other in all seasons (Fig. 12). Interstitial water in the central area with high chlorinities in bottom water in summer maintains comparatively high chlorinities in all seasons.

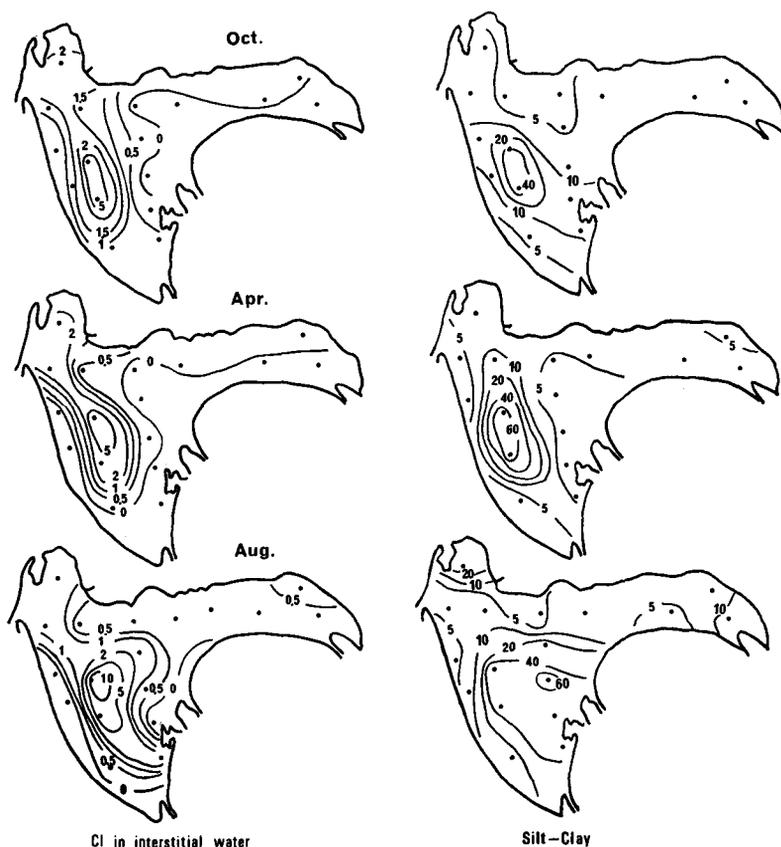


Fig. 12. Seasonal changes in the horizontal distributions of interstitial water chlorinity (‰-Cl) (left) and of silt-clay content (%) (right) larger than 4ϕ in grain diameter in the sediment in Lagoon Zyusan-ko.

As known from Fig. 12, the distribution of interstitial chlorinities is completely similar to that of silt-clay fraction in sediment. The results described above will show that high interstitial chlorinities replaced by permeance of high bottom water chlorinities in summer are supported by very fine sand, i.e. clay and silt in all seasons.

(2) Notoro-ko

Needless to say, water environment was changed after the construction of the opening in 1974, and the interchange with outer sea water is visible in all seasons. As seen in Fig. 13 showing the distributions of oxygen saturation of four cross sections from the opening area to the inner in summer 1968, the degree of saturation decreases suddenly at a water layer of ca. 10 m in depth and at layer deeper than 15 m, showing 30 % saturation at the stations near the opening and zero % at the stations locating from the central to the inner areas. Decreasing of oxygen content with the increase of depth can be noted toward the inner parts but the compensation depth where shows less than 50 % in saturation is ca. 12 m in all sections. This phenomenon of O₂-deficiency in the deeper water in the summer stagnation

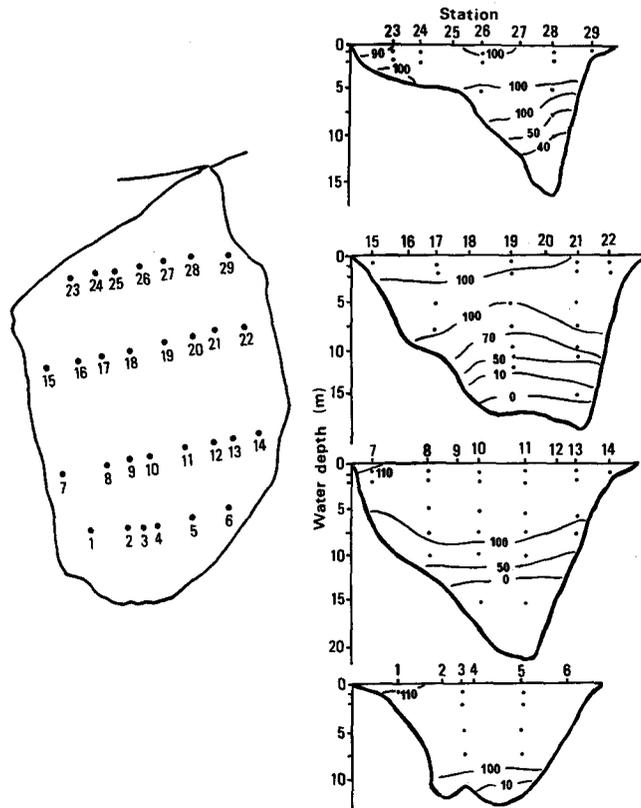


Fig. 13. Sectional diagram showing the vertical distributions of oxygen-saturation (%) in August 1968 in Lake Notoro-ko.

period is not observed in another seasons when a water circulation is active (Fig. 14). After the construction of the mouth, inflow of Okhotsk Sea water and outflow of the lake water through the enlarged opening increase abruptly throughout the year. The seasonal variations in the lake before and after this construction in vertical temperature, chlorinity and dissolved oxygen gradients are shown in Fig. 14. Station 1 is situated at the inner part with a depth of approximately 12 m, and Station 9 at the eastern central part with 20 m depth. In winter 1972 vertical water temperature in the sampled stations is distributed isothermally showing -1°C from surface to bottom. Weak chlorinity gradient occurs and oxygen saturation decreases slightly toward the bottom. In spring 1972 stronger water temperature gradient occurs at these stations and the temperature lowers down from surface to bottom. Vertical distributions of chlorinity and oxygen are similar to those in winter. During the summer in 1972 a definite thermocline develops and is

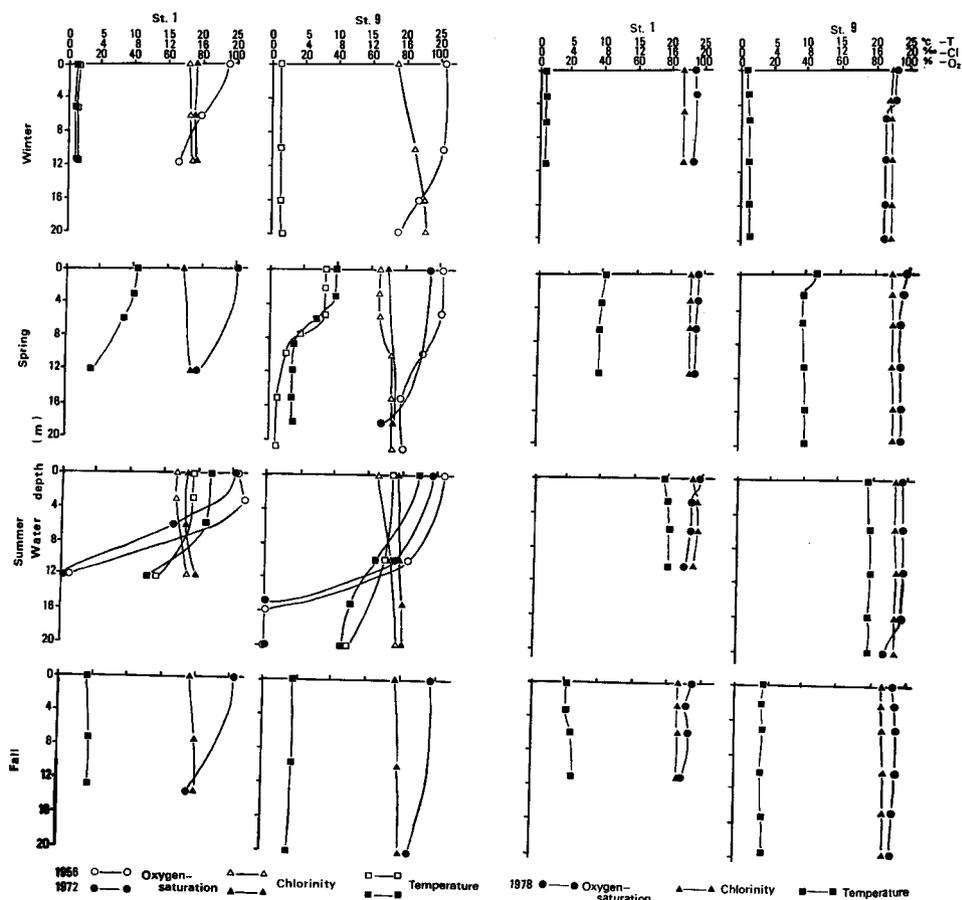


Fig. 14. Seasonal changes of profiles of dissolved oxygen (%), chlorinity (‰) and temperature ($^{\circ}\text{C}$) at the Station 1 situated at the inner part and the Station 9 near the mouth.

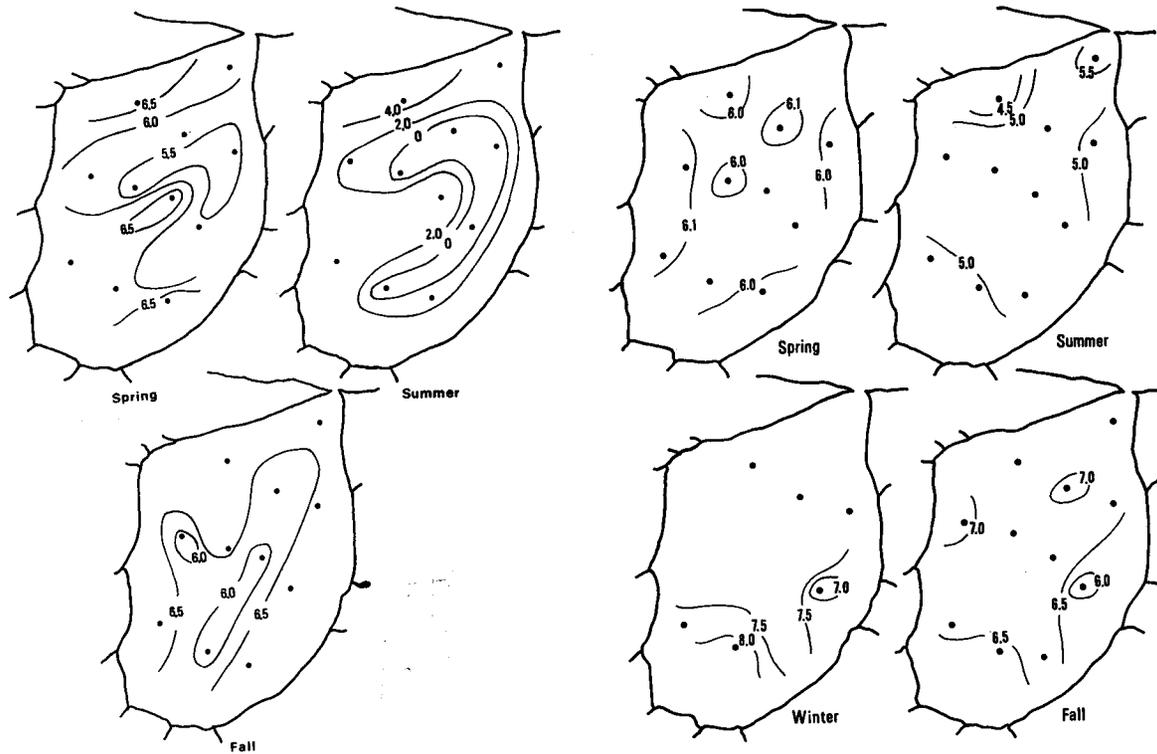


Fig. 15. Seasonal changes in the horizontal distributions of dissolved oxygen content (O₂-ml/l) in bottom water in Lake Notoro-ko before (left) and after (right) the mouth was artificially constructed.

stabilized in part by the appearance of a halocline. The oxygen decreases markedly in the layer deeper than 10 m. Especially at Station 9, a complete lack of oxygen occurs in the layer deeper than 15 m. In fall 1972 this tendency is similar to that in winter except water temperature. After 1974, the topographic changes would have affected upon the quality of the lake water. A thermocline and low oxygen content which occurred during the summer 1972 are not observed afterwards. When the water column is not stratified, it is well oxygenated from surface to bottom. From this fact, we may safely conclude that the differences in vertical chlorinity, water temperature and oxygen content can be scarcely recognized between

Table 3. Water quality in Hakodate Bay. upper row: surface water, under row: bottom water

St	Aug. 1970				Feb. 1971			
	Depth m	Temp °C	Cl ‰	DO ppm	Depth m	Temp °C	Cl ‰	DO ppm
1	7	18.1	18.36	6.0	12	5.5	18.13	8.2
		18.0	18.42	6.0		5.6	18.14	7.7
2	—	—	—	—	10	5.7	18.13	8.1
		—	—	—		6.0	18.16	7.9
3	—	—	—	—	9.5	5.1	18.10	8.1
		—	—	—		5.8	18.10	8.0
4	10	18.4	18.31	8.2	10	5.7	18.10	8.3
		18.2	18.64	7.8		5.7	18.13	7.8
5	5	19.5	18.39	8.4	6	5.7	18.10	8.3
		18.5	18.54	7.8		5.8	18.13	7.8
6	8.5	18.6	18.23	7.0	14.5	6.0	18.18	8.2
		18.4	18.52	7.2		6.2	18.21	8.2
7	20	18.4	18.49	8.2	19.5	5.9	18.16	9.0
		18.7	18.55	8.1		6.0	18.16	7.9
8	—	—	—	—	18	6.1	18.29	8.9
		—	—	—		6.5	18.52	8.0
9	10	19.0	18.10	7.6	11	6.0	17.93	8.8
		17.8	18.70	7.6		6.0	18.13	8.1
10	5	18.9	18.40	8.7	5	5.6	17.82	8.4
		19.0	18.59	8.2		5.6	18.04	8.1
11	5	19.1	18.41	8.5	4	5.8	18.02	8.7
		19.0	18.34	7.6		5.9	18.27	8.5
12	7.5	19.30	17.94	8.2	8	5.8	18.04	8.8
		18.80	18.50	7.4		5.9	18.16	8.0
13	10	18.90	18.04	8.3	11	6.2	18.38	8.9
		18.20	18.52	8.1		6.3	18.40	8.0
14	4.4	19.5	17.87	8.4	5.5	5.8	18.07	8.4
		20.0	18.35	8.6		6.1	18.21	7.9
15	3.5	19.5	17.95	8.0	4.5	5.9	18.11	8.6
		—	18.46	7.6		6.2	18.13	8.0
16	5	19.6	17.95	8.4	5	6.0	17.99	9.0
		19.5	18.52	7.8		6.2	18.07	8.7

surface and bottom. The chlorinity observed in summer, however, is 1 ‰ higher than that in winter. Characteristics and their changes in dissolved oxygen condition of the water column as described above are also found to be horizontal in it of bottom water (Fig. 15). The figure shows that in summer 1972 oxygen is deficient in bottom water from the opening to the inner part with the deepening lower than 10 m, and a complete lack of oxygen occurs in bottom water at layer deeper than 12 m. In 1978 there is no difference in the spatial and temporal distributions of oxygen in bottom water, and they are stable showing comparatively high values ranging from 5 ml-O₂/l in summer to 7-8 ml-O₂/l in winter.

(3) Hakodate Bay

Hakodate Bay which faces the Straits of Tsugaru seems to be influenced by the oceanographical factors caused by Tsugaru Current. Hence, the seasonal distributions of temperature, chlorinity and dissolved oxygen seem to be identical in space. In Table 3 are shown temperatures, chlorinities and oxygen quantity in the surface and the bottom water in summer and winter sampled at the stations as shown in Fig. 16. It is clear that various values of the water elements in summer do not differ at surface and bottom at the stations sampled except a slightly low oxygen content observed at the inner station in Hakodate Harbor. However, as compared the results obtained in winter with those obtained in summer, chlorinities in winter are lower, while, oxygen contents are higher, though the differences in those values are extremely small. Generally speaking, water elements in Hakodate Bay vary very slightly in time and space.

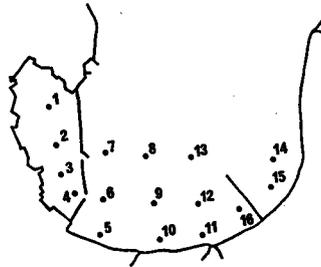


Fig. 16. Map showing the situations of the sampling stations in Hakodate Bay.

3. Discussion

Such vertical and discontinuous gradients in summer as low chlorinity waters shallower than 1.5 m in depth and high chlorinity in waters deeper than 1.5 m as seen in Zyusan-ko, and low chlorinity and high oxygen above the definite thermocline around 10 m in depth and high chlorinity and low oxygen below it as seen in Notoro-ko are decidedly caused by the water circulations. Characteristics of the water elements in the vertical distributions at the stations shown above correspond to those of the horizontal distributions of the sediment as shown in the distributions of interstitial chlorinities in Zyusan-ko and those of organic matter and total

sulfide in Notoro-ko. This fact is also understood from the results that the contents of organic matter and total sulfide in sediment in Notoro-ko decrease markedly and is distributed equivalently in time and space after the opening was artificially constructed, and vertical gradients of water elements disappear. In Hakodate Bay with small differences in the vertical distributions of the water elements in space and time, the horizontal distributions of the sediment also show only a little spatial differences which might be mainly influenced by the depth or the bottom topography. As already described, environments in Hakodate Bay are stable in time and space, but are seasonally and spatially largely variable in Zyusan-ko and Notoro-ko. It may be said that chlorinity in Zyusan-ko and oxygen and sulfide contents in Notoro-ko before 1972 when the opening was constructed represent the important limiting factors, namely, benthos in Zyusan-ko may tolerate the changes in chlorinity and in Notoro-ko before 1972 low oxygen content in bottom water in summer and high sulfide content in sediment in all seasons. Of course, the degree of influence of these limiting factors on benthos may depend on species and the amount of contents. On the other hand, in Hakodate Bay there may not be the limiting factors of the water and the sediment for the occurrence of benthos from the physiological viewpoint.

IV. Structure of benthic communities

Since benthos depend upon environment in which they inhabit, directly and indirectly (Miyadi, et al., 1944; Habe, 1956; Sanders, 1958, 1968; Horikoshi, 1962, 1970), different environment induces different species or community structures. Therefore, the structure of benthic community in each area in time and space must be clarified in order to determine the relationships between benthic communities and environment. As the characteristics of the structures of benthic communities are controlled by the population dynamics, dominant species with a large number of individual in the areas investigated must first be examined and then their temporal and spatial distributions must be described. Secondly, the characteristics of the structure of benthic community which is any assemblage of populations living in a prescribed area can be understood on a basis of the community type and species diversity that may be attributed to the benthic community.

1. *Species compositions and the distributions of dominant species in time and space*

(1) Zyusan-ko

As is evident from Table 4 showing the average count of animals per station in each month, 17 species are collected in total in this study, which are composed of 5 species of polychaetes and amphipods respectively, 4 species of mollusks, 2 species of nemertians and 1 species of sipunculoid. Of these, species with abundant occurrence are the freshwater clam *Corbicula japonica*, two species of polychaetes, *Heteromastus similis* and *Prionospio japonicus*, the anthurid *Cyathura muromiensis* and Nemertinea A. The polychaete *Notomastus latericeus* is seasonal in occurrence, absent in samples during the cold months but very abundant in other months. Six species listed with more than 50 individuals per square meter are the principal members of benthic communities in Zyusan-ko, and

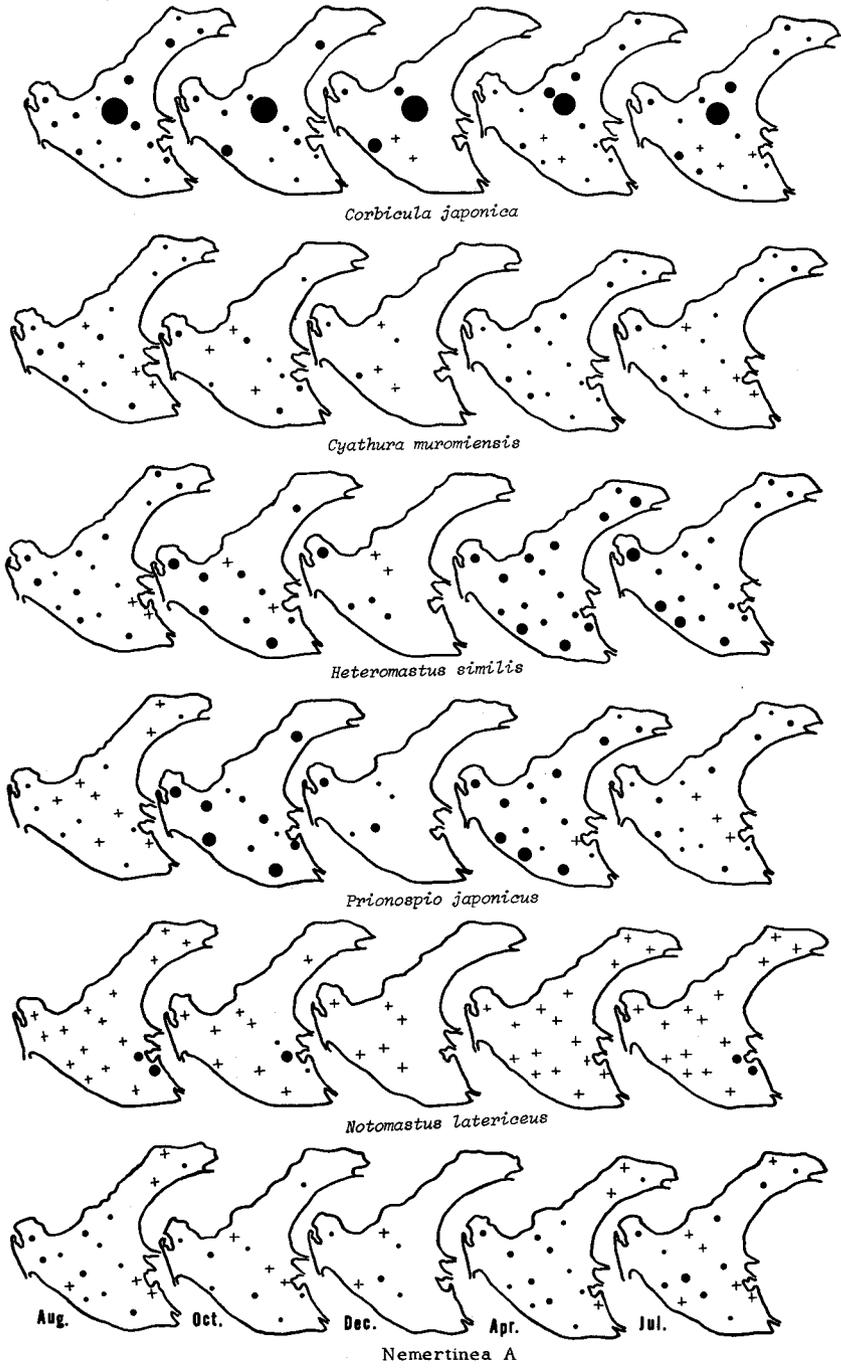
Table 4. Mean number of individuals of benthic fauna per 1 m² in each mouth in Lagoon Zyusan-ko.

Species	Aug.	Oct.	Dec.	Apr.	Jul.
<i>Corbicula japonica</i>	1312	4372	11732	878	850
<i>Assiminea septentrionalis</i>	—	—	—	20	1
<i>Mya arenaria oonogai</i>	1	—	—	—	—
<i>Cyathura muromiensis</i>	68	80	65	70	69
Gammaridae A	3	15	—	—	—
B	—	5	18	—	3
C	—	5	—	—	—
Chironomidae	—	—	—	—	4
<i>Heteromastus similis</i>	192	686	327	743	695
<i>Notomastus latericeus</i>	120	141	—	—	103
<i>Prionospio japonicus</i>	15	1116	305	723	86
<i>Nereis japonicus</i>	14	36	40	26	41
<i>Sigambra</i> sp.	13	5	7	5	11
<i>Urechis</i> sp.	5	2	7	1	—
Nemertinea A	61	57	70	130	135
Nemertinea B	—	—	—	16	6

their distributions are shown in Fig. 17. *C. japonica* occurs more abundantly and rather widely in both the eastern and the western regions of the lagoon except the central deep area. *C. muromiensis* occurs in the same habitat as *C. japonica*. *H. similis* occurs in fairly large number in the western part of the lagoon, more or less distributing in the whole areas. Nemertinea A is only distributed in the central deep area. These 4 species listed above do not show the areal and temporal distributions, whereas, two species of polychaetes occur seasonally, one is *P. japonicus* which has a distribution center in the western side of the lagoon from fall to spring; it is rare in summer. The other, *N. latericeus*, occurring only in warmer months is found only in the small region of the mouth of the Iwaki River.

(2) Notoro-ko

The average individual number of animals per station in each season in 1972 is given in Table 5. Dominant species with over 50 individuals per square meter are two species of polychaetes, *Prionospio malmgreni* and *Dorvillea japonica*, the pelecypod *Musculus senhousia*, the gastropod *Mitrella tenuis*, the amphipod *Ampelisca brevicornis* and the chironomid *Pseudochironomus* sp. In addition, the polychaete *Platynereis bicanaliculata* is seen from fall to spring, and the anthurid *Paranthura japonica*, three species of polychaetes *Cistenides soldatovi*, *Glycinde* sp. and *Sigambra tentaculata* occur rather abundantly in all seasons. The areal and temporal distributions of six dominant species are shown in Fig. 18, which indicates two significant characteristics. One is the fact that there is no occurrence of organisms in an area deeper than 15 m all the year round as it is called the azoic zone, and the other is that all of the six species show a restricted distribution. *P. malmgreni* occurs in rather abundantly from winter to spring, and *D. japonica* is similar in its seasonal distribution to that of *P. malmgreni*, but its areal distribution is more restricted than that of *P. malmgreni*, that is to say, it occurs only in the neighboring



● >10000, ● 10000-5000, ● 5000-3000, ● 3000-1000, ● 1000-500, ● 500-100, +100-1, +0

Fig. 17. Map showing the distributions of number of individuals per m² for six common benthic animals in Lagoon Zyusan-ko.

Table 5. Seasonal numbers of individuals of benthic animals per 1 m² observed in Lake Notoro-ko in 1972 before the mouth was artificially constructed.

Species	Summer	Fall	Winter	Spring
<i>Harmothoe imbricata</i>	1	1	1	1
<i>Chrysopetatum occidentale</i>	1	1	-	-
<i>Anaitides maculata</i>	-	1	-	-
<i>Eteone longa</i>	-	1	-	-
<i>Sigambra tentaculata</i>	11	14	14	21
Syllidae	-	1	-	1
<i>Nereis zonata</i>	1	-	-	1
<i>Glycinde</i> sp.	7	9	5	8
<i>Glycera alba</i>	-	1	1	-
<i>G. tessellata</i>	-	-	1	-
<i>Lumbrineris japonica</i>	12	5	1	6
<i>Pseudopolydora kempfi japonica</i>	1	3	1	3
<i>Laonice cirrata</i>	3	9	8	4
<i>Prionospio malmgreni</i>	60	1275	155	527
<i>P.</i> sp.	-	-	1	-
Cirratulidae	-	1	-	-
<i>Cirratulus cirratus</i>	-	-	-	1
<i>Capitella capitata</i>	3	1	6	-
<i>Pherusa plumosa</i>	-	-	1	1
<i>Scalibregma inflatum</i>	-	-	1	1
<i>Heteromastus giganteus</i>	3	4	2	6
<i>Owenia fusiformis</i>	3	-	1	-
<i>Cistenides soldatovi</i>	56	46	12	9
<i>Melinna elisabethae</i>	1	1	2	-
<i>Ampharete arctica</i>	-	-	-	4
<i>Pseudosabellides littoralis</i>	2	6	2	4
<i>Chone</i> sp.	1	1	1	3
<i>Pista</i> sp.	1	2	5	-
<i>Dorvillea japonica</i>	30	160	146	92
<i>Spiophanes bombyx</i>	-	-	-	1
<i>Magelona japonica</i>	-	-	-	1
<i>M.</i> sp.	-	1	-	-
<i>Protodorvillea gracilis</i>	-	4	-	1
<i>Spio filicornis</i>	1	-	1	-
<i>S.</i> sp.	1	-	-	-
<i>Maldane</i> sp.	-	-	1	-
<i>Macoma</i> sp.	20	10	-	7
<i>Masculus senhousia</i>	2	3	7	6
<i>Patenopecten yessoensis</i>	1	-	1	-
<i>Cadella lubrica</i>	-	1	-	1
<i>Neverity didyma</i>	1	1	-	-
<i>Lyonsia ventricosa</i>	2	1	2	-
<i>Tectonatica janthostomoides</i>	9	-	-	1
Pelecypoda	22	52	3	15
<i>Clinocardium californiense</i>	-	-	-	1
<i>Theora lata</i>	-	50	8	23
<i>Mercenaria stimpsoni</i>	1	-	1	-
<i>Mya arenaria oonogai</i>	1	-	-	-
<i>Yoldia thraciaeformis</i>	1	-	-	-
<i>Y. notabilis</i>	2	1	2	1
<i>Niotha livescens</i>	1	-	-	-
<i>Glycymeris yessoensis</i>	-	-	1	2

Table 5. (Continued)

Species	Summer	Fall	Winter	Spring
<i>Mitrella tenuis</i>	352	3146	673	1135
<i>Ampelisca brevicornis</i>	1	6	6	3
<i>Pseudochironomus</i> sp.	3	504	279	572
<i>Paranthura japonica</i>	-	-	1	2
<i>Caprella</i> sp.	-	18	14	27
<i>Tecticeps japonicus</i>	-	1	-	-
Nemertinea A	18	10	9	15
Nemertinea B	15	17	6	15
<i>Amphioptus ancistrotus</i>	29	17	6	16

area of the opening and in the inner part. In contrast to these two species, *M. senhousia* is rare in areas deeper than 6 m, and occurs in large numbers in the shallow waters, especially densely on the shore with ca. 2 m depth in three seasons excluding winter. The areal distributions of *M. tenuis*, *Pseudochironomus* sp. and *A. brevicornis* coincide with that of *M. senhousia*. *M. tenuis*, however, occurs more abundantly in fall, and *Pseudochironomus* sp. occurs from winter to spring. *A. brevicornis* occurs evenly in any seasons.

Their distributions in 1978 are shown in Table 6. As compared it with that in 1972, some differences are observed. The first is the disappearance of the azoic zone in area deeper than 15 m depth, and the second is the diminution in number of the dominant species, and the last is the decline in degree of geographic isolation of the species habitat.

A. brevicornis and *M. senhousia* decrease in number of individuals, therefore, dominant species are *M. tenuis*, *D. japonica*, *P. malmgreni* and *Pseudochironomus* sp. *M. tenuis* and *D. japonica* show a distinct difference in the areal and temporal distributions as compared with those in 1972, namely, *M. tenuis*, occurring in large numbers in the shallow area, and *D. japonica*, occurring in narrow area near the opening and in the inner part in limited seasons in 1972, enlarge their occurrence to cover the whole area in the lake more abundantly in all seasons in 1978. In 1978, *P. malmgreni* shows a similar tendency in the seasonal changes but more abundantly than that in 1972, but extends its occurrence to the area deeper than 6 m. *Pseudochironomus* sp. doesn't show certain differences in the distributions between 1972 and 1978 both in time and space, though no extremely dense concentration is observed in 1978 (Fig. 19).

(3) Hakodate Bay

Dominant species which can be counted over 50 individuals per square meter attains 8 in species, consisting of the polychaetes *Chaetozone* sp., *Cirratulus cirratus*, *Lumbrineris* sp., *Nephtys caeca*, *Capitella capitata*, the gammaridean amphipods Gammarid A and Gammarid B and the pelecypod *Mactra sinensis carneopicta*. The other 5 species of the polychaetes *Prionospio pinnata* and *Scoloplos* sp., the gammaridean amphipods Gammarid C and Gammarid D and the pelecypod *Yoldia excavata* are comparatively large abundant in occurrence (Table 7).

Fig. 18. Seasonal distributions of number of individuals (no./m²) of five common animals in Lake Notoro-ko in 1972 before the mouth was artificially constructed. Symbols as in Fig. 17.

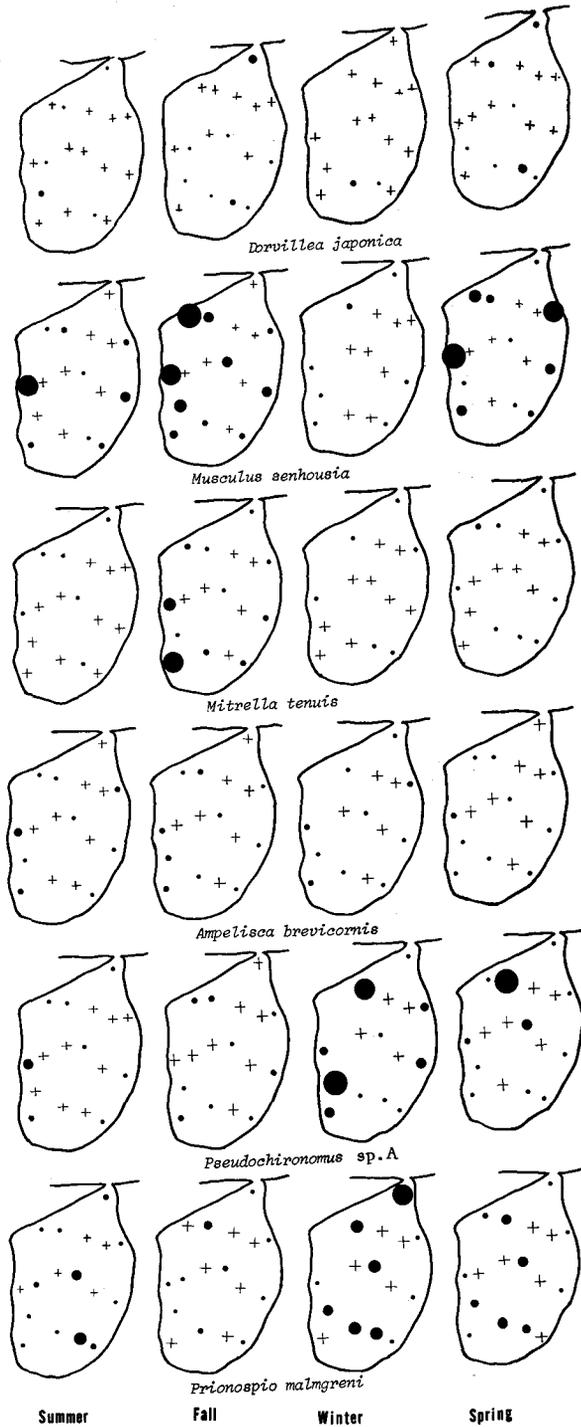


Table 6. Seasonal number of individuals of benthos per 1 m² taken in Notoro-ko in 1978 after the mouth was artificially constructed.

Species	Summer	Fall	Winter	Spring
<i>Harmothoe imbricata</i>	21	4	3	3
<i>Chrysopetalum occidentale</i>	1	1	1	1
<i>Anaitides maculata</i>	1	2	1	1
<i>Eteone longa</i>	1	-	-	1
<i>Sigambra tentaculata</i>	16	8	35	33
<i>Syllis</i> sp.	1	-	-	-
<i>Nereis zonata</i>	1	1	3	4
<i>N. japonica</i>	1	-	-	-
<i>Platynereis bicanariculata</i>	2	18	18	1
<i>Glycinde</i> sp.	6	3	19	11
<i>Glycera alba</i>	-	1	-	-
<i>Lumbrineris</i> sp.	2	1	6	1
<i>Dorvillea japonica</i>	16	17	63	70
<i>Pseudopolydora kempii japonica</i>	7	3	9	5
<i>Laonice cirrata</i>	9	3	9	6
<i>Prionospio malmgreni</i>	326	132	1243	374
<i>Spio borealis</i>	-	-	2	-
<i>Pherusa plumosa</i>	-	-	1	25
<i>Scalibregma inflatum</i>	1	3	2	-
<i>Ophelia limacina</i>	1	3	3	-
<i>Capitella capitata</i>	1	2	1	37
<i>Capitella</i> sp.	9	2	2	-
<i>Heteromastus giganteus</i>	3	1	3	1
<i>Maldane</i> sp.	9	8	14	1
<i>Owenia fusiformis</i>	-	-	1	-
<i>Cistenides soldatovi</i>	5	44	3	30
<i>Ampharete arctica</i>	1	1	3	5
<i>Melinna elisabethae</i>	2	3	3	20
<i>Magelona japonica</i>	6	-	-	-
<i>Chone</i> sp.	1	-	-	-
<i>Pseudosabellides littoralis</i>	1	1	3	55
<i>Pista</i> sp.	5	6	5	23
<i>Mactra</i> sp.	8	6	-	-
<i>Macoma</i> sp.	2	12	1	2
<i>Musculus senhousia</i>	481	1576	23	1587
<i>Clinocardium californiense</i>	6	1	-	2
<i>Mitrella tenuis</i>	5	685	3	11
<i>Tiberia</i> sp.	-	-	1	-
<i>Phodopetoma</i> sp.	-	-	1	-
<i>Ampelisca brevicornis</i>	68	52	49	22
Gammaridae	-	1	8	1
<i>Tecticeps japonicus</i>	1	1	-	-
<i>Pseudochironomus</i> sp. A	83	86	1811	906
<i>Paranthura japonica</i>	9	8	8	2
<i>Caprella</i> sp.	14	73	2	28
Cumacea A	29	1	-	2
Cumacea B	-	5	1	-
Nemertinea A	8	5	7	10
Nemertinea B	15	21	20	23
<i>Phoronis</i> sp.	-	-	39	0
<i>Asterias amurensis</i>	3	-	1	1
<i>Amphioplus ancistrotus</i>	2	2	10	5

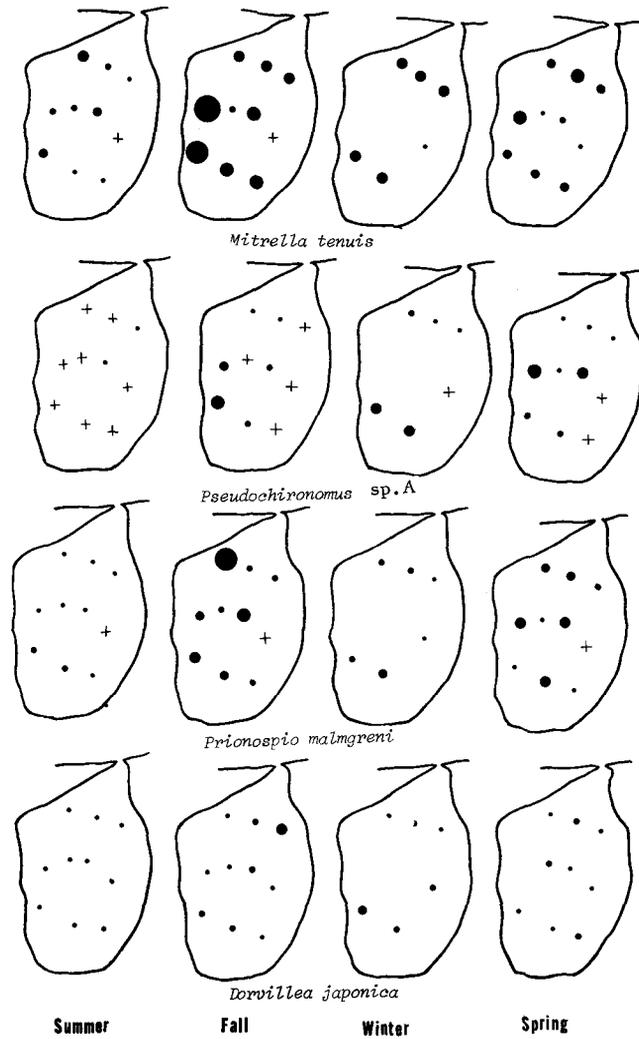


Fig. 19. Map showing the seasonal distributions of number of individuals (no./m²) of four common benthic fauna in Lake Notoro-ko in 1978 after the mouth was artificially constructed. Symbols as in Fig. 17.

As is evident from Fig. 20 which shows the areal and temporal distributions of the 8 dominant species, *Chaetozone* sp. occurs in large numbers in the inner part of Hokodate Harbor and in the central region of Hokodate Bay, and in small numbers on the shallow shore. The distributions of *C. cirratus*, *C. capitata* and *Lumbrineris* sp. mostly coincide with that of *Chaetozone* sp.. Of these four, *Lumbrineris* sp. shows the most restricted distribution, and, as can be seen in Fig. 20, it is found only in the relatively small area from Hakodate Harbor to the central part of the bay. On the other hand, the polychaete *N. caeca* is rather

Table 7. Seasonal number of individuals of benthic animals per 1 m² sampled in Hakodate Bay.

Species	Summer	Fall	Winter	Spring
<i>Chaetozone</i> sp.	405	301	472	158
<i>Cirratulus cirratus</i>	156	222	115	29
<i>Lumbrineris</i> sp.	85	104	134	25
<i>Diopatra sugokai</i>	3	2	-	-
Flabelligeridae	34	32	4	4
<i>Chone</i> sp.	6	10	6	6
<i>Pseudopotamilla</i> sp.	-	1	-	-
<i>P. ocellata</i>	1	-	-	-
<i>Magelona japonica</i>	17	17	33	15
Magelonidae	1	1	-	-
<i>Magelona</i> sp.	-	-	-	18
<i>Nephtys caeca</i>	100	135	77	47
Spionidae	3	3	-	-
<i>Prionospio pinnata</i>	29	52	-	-
<i>P. japonica</i>	-	-	21	-
<i>P. krusadensis</i>	-	-	2	27
<i>Laonice</i> sp.	5	5	4	14
<i>Spio borealis</i>	7	4	-	-
<i>S. filicornis</i>	-	-	-	2
<i>Eteone longa</i>	-	-	-	1
<i>Glycera chirori</i>	35	8	7	9
<i>G. alba</i>	2	21	-	1
<i>Glycinda</i> sp. A	-	-	1	12
<i>G.</i> sp. B	-	-	8	4
<i>Eumida sanguinea</i>	3	3	12	2
<i>Goniada</i> sp.	35	17	-	1
<i>Ophiodromus puggettensis</i>	-	-	-	1
<i>Anaitides maculata</i>	13	6	4	6
<i>Phyllodoce</i> sp.	-	41	-	-
<i>Amage auricula</i>	33	3	-	-
<i>Amphicteis gunneri</i>	10	4	-	-
<i>Scoloplos armiger</i>	-	-	1	2
<i>S.</i> sp.	15	61	5	-
Hesionidae	4	22	-	-
<i>Terebellides stroemii</i>	-	-	1	5
Terebellidae	9	12	-	-
<i>Harmothoe imbricata</i>	-	-	2	-
<i>Tharyx</i> sp.	-	-	1	13
<i>Maldane sarsi</i>	-	-	12	19
Maldanidae	27	14	1	-
<i>Neanthes diversicolor</i>	-	-	1	2
<i>N.</i> sp.	2	2	-	-
<i>Ophelia limacina</i>	-	-	8	33
Ophelidae	8	2	-	-
<i>Scalibregma inflatum</i>	1	-	-	-
<i>Syllis</i> sp.	1	10	-	-
<i>Chloëia</i> sp.	3	4	-	-
<i>Aphrodita japonica</i>	-	-	-	2
<i>A.</i> sp.	1	-	-	-
<i>Capitella capitata</i>	196	170	197	67
<i>Pseudopolydora kempfi</i>	-	1	-	-
<i>Hydroides ezoensis</i>	-	-	1	-
<i>H.</i> sp.	1	1	-	-

Table 7. (Continued)

Species	Summer	Fall	Winter	Spring
Sipunculida	100	94	1	2
Gammarid A	1400	693	407	165
B	597	167	78	27
C	121	59	30	11
D	70	21	4	2
E	25	13	6	4
Cummacea	-	-	12	4
Amphipoda	20	12	1	6
Pycnogonida	-	-	2	6
Ophiuroidea	9	9	-	-
Echinoidea	1	1	-	-
<i>Mactra sinensis carneopicta</i>	57	31	65	136
<i>Spisula sachalinensis</i>	4	31	2	22
<i>Yoldia excavata</i>	16	51	3	41
<i>Macoma</i> sp.	9	30	-	2
<i>Masculus senhousia</i>	-	-	-	1
Polyplacophora	-	-	-	2
<i>Fabulina nitidula</i>	-	-	-	1
<i>Clinocardium californiense</i>	-	-	2	1
<i>Ophioplocus japonica</i>	-	-	10	11
<i>Theora lata</i>	3	4	1	2
<i>Patinopecten yessoensis</i>	1	-	4	10
Protochordata	3	9	-	-
Nemertinea A	-	-	2	-
B	-	-	6	-
C	1	2	-	-
Coelenterata	-	-	2	1

contrary in occurrence to the four polychaetes listed above, distributing in large number in the shallow water, and in small number in the areas which have large number of the four polychaetes. These five dominant species do not show any changes in their areal and temporal distributions. However, *M. sinensis carneopicta* and two gammarids are seasonal in distribution, occurring densely in spring and summer ranging from the central part to the shore.

2. Community types and their distributions in time and space

If the nature of a few samples taken from broad areas are very similar to one another in species composition and their individual numbers, it may be considered that these samples are extracted from the same type community. The areal extent of these samples, therefore, can be deemed as that of the same type community. On the contrary, the differences in species compositions and in the areal extents of communities classified according to the community types will be a reflection of the biotic or physical environmental factors. Consequently, the aspects of areal and temporal distributions of benthic communities should be examined first.

Many indices have been devised for determining the degree of similarity between the samples. However, they have mostly a disadvantage in that the values obtained are considerably influenced by the average number of individuals, number

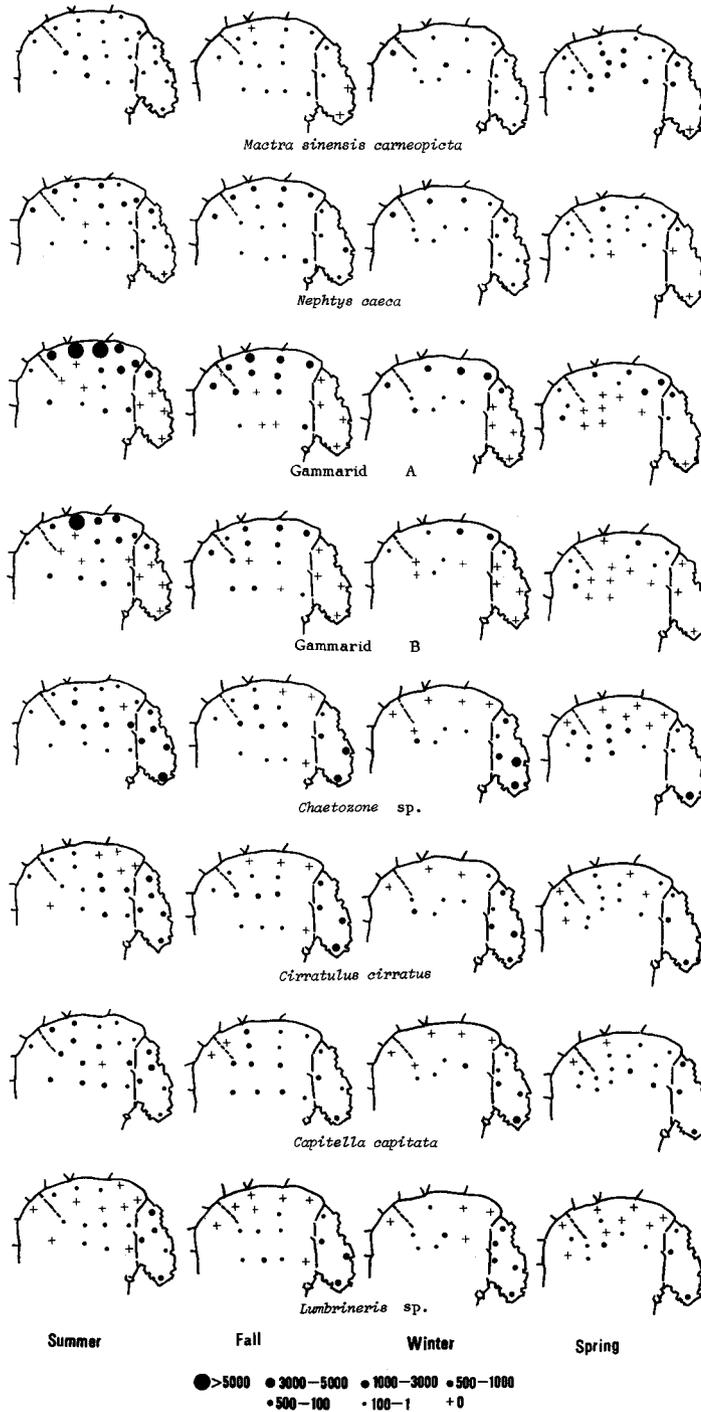


Fig. 20. Map showing the seasonal distributions (no. of ind./m²) of eight common animals in Hakodate Bay. Circles indicate the number of individuals per 1 m².

of individuals of dominant or rare species as has been partly noticed by Morisita (1959) and Aoki (1962). In this paper, Morisita's similarity index (Morisita, 1959) is applied to measure similarity among samples in order to eliminate disadvantage mentioned above. It is almost unaffected, though not perfectly, by the sample size employed for measuring similarity between samples. Morisita's index is indicated as follows:

$$C_{\lambda} = 2 \sum_{i=1}^{\infty} n_{1i} n_{2i} / (\lambda_1 + \lambda_2) N_1 N_2$$

$$\lambda_1 = \sum_{i=1}^{\infty} n_{1i}(n_{1i}-1) / N_1(N_1-1)$$

$$\lambda_2 = \sum_{i=1}^{\infty} n_{2i}(n_{2i}-1) / N_2(N_2-1)$$

Where N_1 and N_2 are the total number of individuals of the samples I and II, and n_{1i} and n_{2i} are the numbers of individuals of species i found in the samples I and II, respectively. The value of C_{λ} will be about 1 when the two samples belong to same community and will be zero when no common species is found between them.

The method adopted for classifying the samples into groups of similar samples is as follows:

$$I = \frac{1}{mn} \sum_{i=1}^m \sum_{j=1}^n I(A_i B_j)$$

Where m and n are the number of sample of the sample group A and B respectively, and $I(A_i B_j)$ is Morisita's index (C_{λ}) between sample i of sample group A and sample j of sample group B (Mountford, 1962).

(1) Zyusan-ko

To obtain the benthic community types based on the classification of the samples in Zyusan-ko, indices of similarity calculated by the formulae of Morisita and Mountford described above are shown in Fig. 21 as a dendrogram.

If the communities is divided by the cluster group of which values are higher than 0.8 in the indices of similarity, five cluster groups can be counted in the dendrogram of August, two cluster groups in October and December, and four cluster groups in April and July. Similarities between the cluster groups of each month are recalculated according to Morisita's formula as showing an instance in Table 8. Consequently, the benthic communities in Zyusan-ko may be divided into eight community types of Cluster groups from A to H through a year. As shown in the dendrogram of August, cluster group A is slightly correlated with Cluster group C, and Cluster group D with Cluster group B, respectively, while, Cluster groups A and C and Cluster groups D and B and Cluster group H are not correlated with one another.

The frequency distributions of 6 species of dominant benthos in the community types are shown in Fig. 22, and the seasonal and areal distributions of communities based on the community types are also shown in Fig. 23. These communities are categorized as follows:

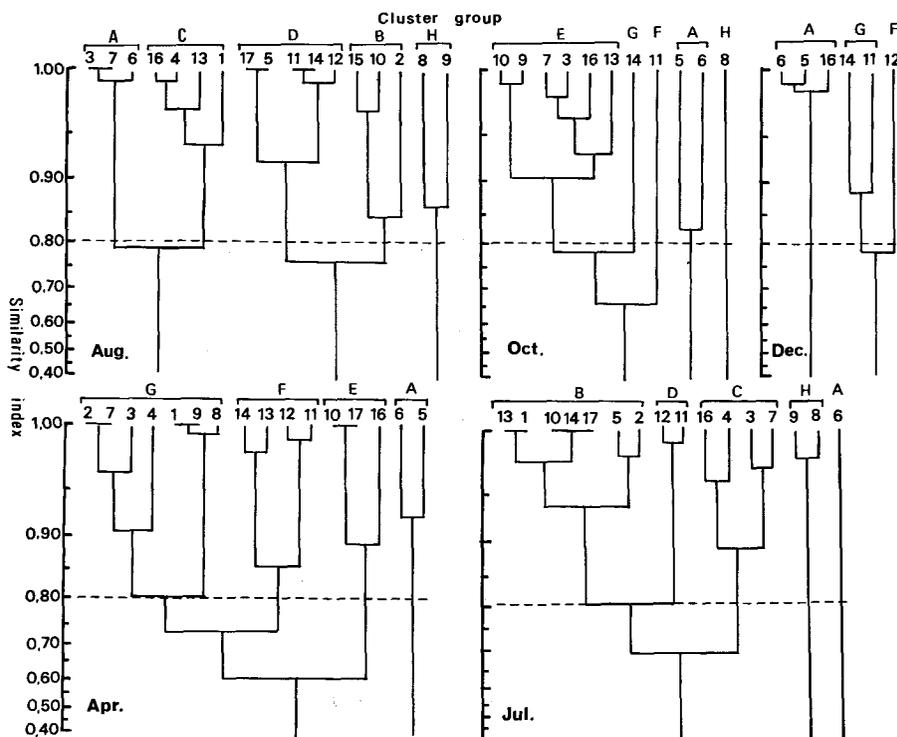


Fig. 21. Plot of results of the cluster analysis as a dendrogram in Lagoon Zyusan-ko. The cluster level at a similarity index values of 0.8 is chosen as the cut-off level for recognition of distinct cluster groups.

A: *Corbicula* type community, B: *Heteromastus* type community, C: *Corbicula* - *Heteromastus* type community, D: *Heteromastus*-*Nemertinea* type community, E: *Corbicula*-*Heteromastus*-*Prionospio* type community, F: *Prionospio*-*Heteromastus*-*Nemertinea* type community, G: *Prionospio*-*Heteromastus*-*Corbicula* type community H: *Notomastus* type community.

Table 8. Similarity index (Moristia's index) of *Corbicula* type communities observed in each month on Lagoon Zyusan-ko.

	Aug.		Oct.		Dec.			Apr.	
	7	6	5	6	5	6	16	5	6
3	0.98	0.96	0.99	1.00	0.98	0.94	0.96	0.98	0.99
7		0.89	0.29	0.87	0.88	0.98	0.86	0.87	0.97
6			0.87	0.90	0.86	0.85	0.89	0.92	0.98
5				0.98	0.87	0.83	0.90	1.00	0.98
6					0.86	0.89	0.95	0.86	0.88
5						0.99	0.96	0.87	0.86
6							1.00	0.93	0.89
16								0.82	0.84
5									1.00
6									

1) Cluster group A (*Corbicula* type community). This community is principally composed of *Corbicula japonica* with composition percentage higher than 50 %, and *Heteromastus similis*, *Cyathura muromiensis* and *Nereis japonica* are faunal elements of this community (Fig. 22). This community occurs in two isolated regions, one in the western shallow water called "Okinose" and the other in the eastern shallow region all the year round.

2) Cluster group B (*Heteromastus* type community). This is principally composed of *H. similis* with composition percentage ranging 40–80 % and of such minor fauna as *C. japonica* and *C. muromiensis*, occurs in the shallow coasts in summer.

3) Cluster group C (*Corbicula-Heteromastus* type community). This is principally composed of *C. japonica* and *H. similis*, occupying the large areal extent only in summer.

Cyathura muromiensis is a common species in the three communities above mentioned (Fig. 22).

4) Cluster group D (*Heteromastus-Nemertinea* type community). This community principally composed of *H. similis* and Nemertinea A, and *C. japonica* and *C. muromiensis* are minor species in this community, occurs in the central deep area of the lagoon in summer.

5) Cluster group E (*Corbicula-Heteromastus-Prionospio* type community). This community is principally composed of *C. japonica*, *H. similis* and *Prionospio japonicus*, occurring from fall to spring in the same area as *Corbicula-Heteromastus* type community which is observed only in summer but has the most restricted distribution only in the western shallow coast in spring as shown in Fig. 23.

6) Cluster group F (*Prionospio-Heteromastus-Nemertinea* type community). This is principally composed of *P. japonicus*, *H. similis* and Nemertinea A, occurring from fall to spring in the same areas as *Heteromastus-Nemertinea* type community which is observed in summer.

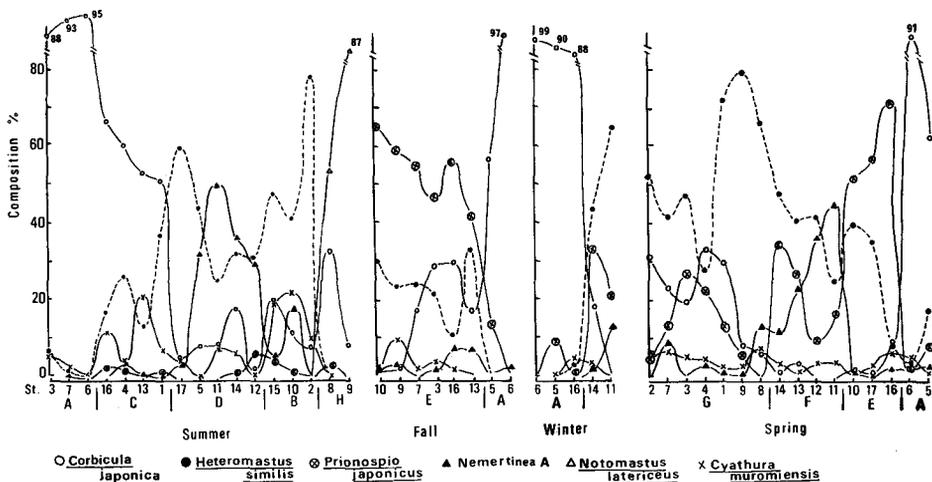


Fig. 22. Map showing the composition percentage of six common species in each community in Lagoon Zyusan-ko. See Fig. 21 for A-H.

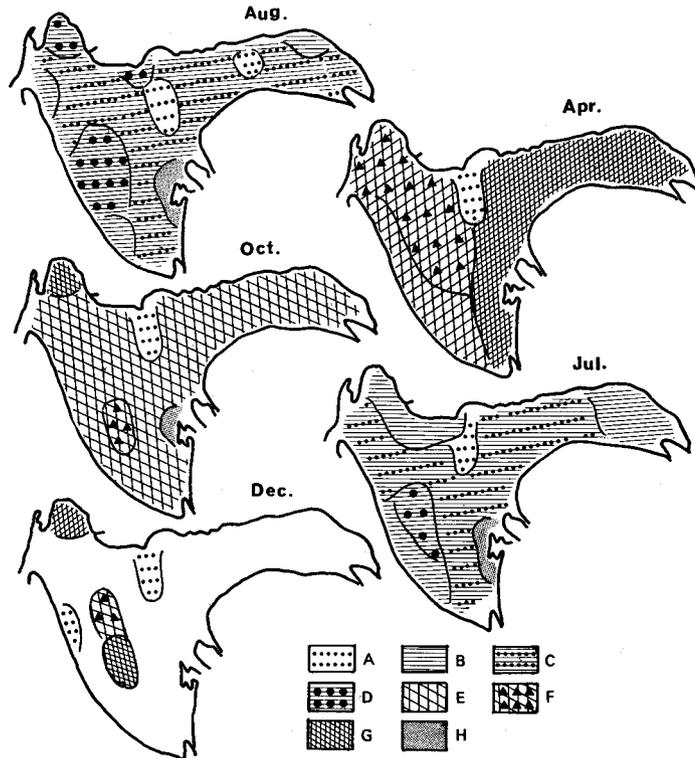


Fig. 23. Seasonal and spatial distributions of benthic communities in Lagoon Zyusan-ko.
See Fig. 21 for A-H.

7) Cluster group G (*Prionospio-Heteromastus-Corbicula* type community). This is somewhat similar to *Corbicula-Heteromastus-Prionospio* type community, though the composition percentage of *P. japonicus* in this community are markedly higher than that of *Corbicula-Heteromastus-Prionospio* type community. However, composition percentage of *C. japonica* is relatively low. This community occurs mostly in spring in the inner area where is the portion of extent of *Corbicula-Heteromastus-Prionospio* type community which is observed in fall.

8) Cluster group H (*Notomastus* type community). This is principally composed of *Notomastus latericeus* with composition percentage higher than 50%, and *C. japonica* is few in number. This community has the most restricted distribution in the neighboring area of the mouth of the Iwaki River in the warm months.

Fig. 23 denotes that in *Corbicula* type community no changes in its distribution are seen both in area and season. On the other hand, *Heteromastus* type community and *Corbicula-Heteromastus* type community observed in summer take the place of *Corbicula-Heteromastus-Prionospio* type community and *Prionospio-Heteromastus-Corbicula* type community found in fall. *Heteromastus-Nemertinea* type community in summer takes the place of *Prionospio-Heteromastus-Nemertinea* type community in seasons from fall to spring. Their areal distributions, however,

coincide with those of each community pair just mentioned above.

Seasonal and spatial changes in species composition and community distributions in Zyusan-ko take place at the season change from summer to fall except those of *Corbicula* type and *Notomastus* type. These changes at the community level may decidedly be controlled by the population densities of *P. japonicus* occurring from fall to spring through winter.

(2) Notoro-ko

In Fig. 24 are shown the dendrograms of the classification of benthic community types in 1972 before the opening was artificially constructed. Four cluster groups are observed in the dendrogram of fall, three in summer and in spring respectively and two in winter. These cluster groups are classified into following eight communities by using the same procedure as in Zyusan-ko, and the distribution frequency of the dominant species in each community are shown in Fig. 25.

1) Cluster group A (*Musculus* type community). This is principally composed of *Musculus senhousia* with composition percentage higher than 50% and predominated by two other species, *Ampelisca brevicornis* and *Pseudochironomas* sp. (Fig. 25). This develops in the area shallower than 2 m depth in spring, and gradually decreases in its extent between summer and fall, disappearing in winter.

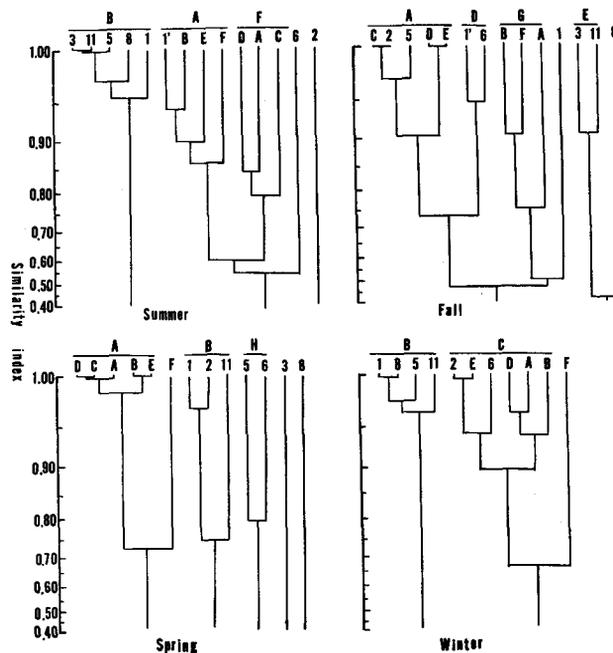


Fig. 24. Plot of results of the cluster analysis as a dendrogram in Lake Notoro-ko in 1972 before the mouth was artificially constructed. A: *Musculus* type community, B: *Prionospio* type community, C: *Pseudochironomus* type community, D: *Musculus-Prionospio* type community, E: *Cistnides* type community, F: *Musculus-Ampelisca* type community, G: *Musculus-Mitrella* type community, H: *Pseudochironomus-Prionospio* type community.

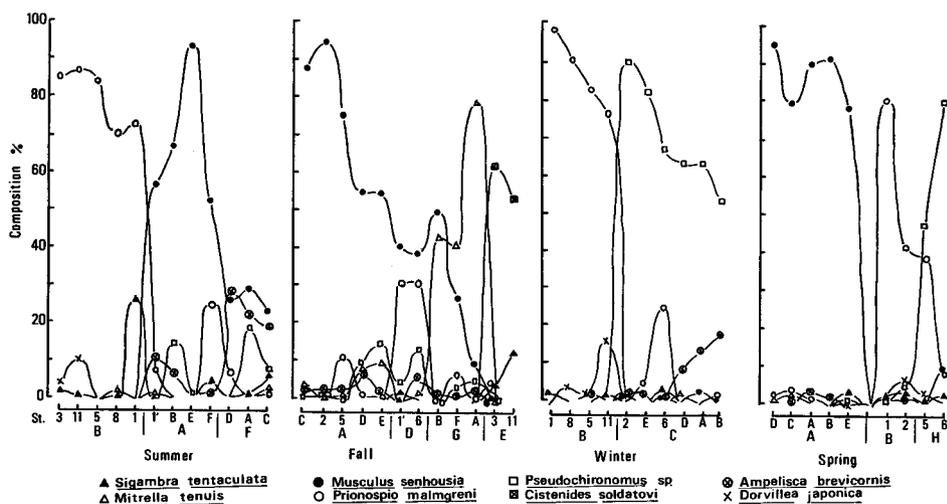


Fig. 25. Map showing the composition percentage of eight common animals in each community in Lake Notoro-ko. See Fig. 24 for A-H.

2) Cluster group B (*Prionospio* type community). This is principally composed of *Prionospio malmgreni* with composition percentage higher than 60%, and predominated by *Dorvillea japonica*, *Sigambra tentaculata* and *Pseudochironomus* sp. This community occurs near the opening and in the central part from winter to summer.

3) Cluster group C (*Pseudochironomus* type community). This is mainly composed of *Pseudochironomus* sp. with high percentage ranging 50–80% and predominated by *A. brevicornis* and *P. malmgreni*. *M. senhousia* rarely appears in this community. This community develops in the areas shallower than 2 m depth in winter, and its extent coincides completely with that of *Musculus* type community in spring.

4) Cluster group D (*Musculus-Prionospio* type community). This community is more or less similar to *Musculus* type community in species composition, being mainly composed of two species with higher than 70% in composition percentage. One is *M. senhousia* and the other *P. malmgreni*. The third species, *Cistenides soldatovi* is also a member of this community. This occurs both in the central and western parts adjoining *Musculus* type community in fall.

5) Cluster group E (*Cistenides* type community). This is composed of only a few species among which *C. soldatovi* is a principal member of this community. This occurs only in fall.

6) Cluster group F (*Musculus-Ampelisca* type community). This is principally composed of *M. senhousia* and *A. brevicornis* with a similar composition percentage to each other, about 50% in total, and somewhat similar to *Musculus* type community in species composition. This community also appears in the coastal areas neighboring the *Musculus* type community only in summer.

7) Cluster group G (*Musculus-Mitrella* type community). This is mainly composed of *Musculus senhousia* and *Mitrella tenuis*, both showing 60–90% in composition percentage and secondarily predominated by *Platynereis bicanaliculata* and

one species of Caprellidae. This community occurs only in the inner parts in fall. 8) Cluster group H (*Pseudochironomus-Prionospio* type community). This is principally composed of *Pseudochironomus* sp. and *P. malmgreni* with composition percentage higher than 85% in both and includes many other species. This community occurs only in the upper and lower parts of the azoic zone in spring.

The areal and temporal distributions of these communities already stated are summarized in Fig. 26.

On the shore shallower than 2 m depth, *Musculus* type community replaces to some extent *Musculus-Ampelisca* type community in summer and *Musculus-Mitrella* type community in fall, both of the latter two types being similar in species composition. This seasonal changes in community types are obviously caused by the increase of population densities of *A. brevicornis* and *M. tenuis* respectively in *Musculus* type community. In winter *M. senhousia* almost disappears and *Pseudochironomus* sp. greatly increases (Fig. 18), therefore, *Pseudochironomus* type community takes the place of *Musculus* type community on the shore. In the

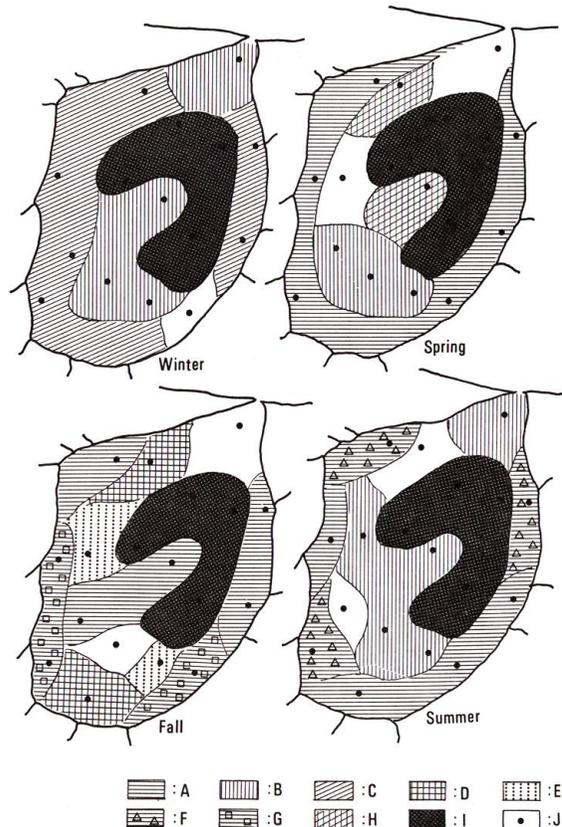


Fig. 26. Map showing the seasonal and the spatial distributions of benthic communities taken in Lake Notoro-ko in 1972. See Fig. 24 for A-H. I: Azoic zone, J: Samples which are devoid of similarity.

areas deeper than 6 m, *Pseudochironomus* sp. and *P. malmgreni* occur abundantly at various stations in three seasons except fall (Fig. 18). *Prionospio* type community and *Pseudochironomus-Prionospio* type community, therefore, occupy the majority of central areas with depth deeper than 6 m in three seasons, but *P. malmgreni*, being rare in fall, *Musculus* type community occurs in the same area.

As is known from Fig. 27, six benthic communities are clearly recognized in Notoro-ko in 1978. The distribution frequency of dominant species in each community are tabulated in Fig. 28.

1) Cluster group H (*Mitrella* type community). This community is principally composed of *M. tenuis*, higher than 50 % in composition percentage, and secondarily predominated by the other three species, *P. malmgreni*, *Pseudochironomus* sp. and *Dorvillea japonica* (Fig. 28).

2) Cluster group B (*Prionospio* type community). This is numerically composed of two species, *P. malmgreni* with 50–60 % in composition percentage and *M. tenuis* with about 30 %, and is closely similar to Cluster group H showing the index value of 0.6 in similarity. This community occurs only in fall in the shallow coastal areas and in the central part.

3) Cluster group I (*Mitrella-Prionospio* type community). This is composed of *M. tenuis* and *P. malmgreni* with composition percentage almost same, and the

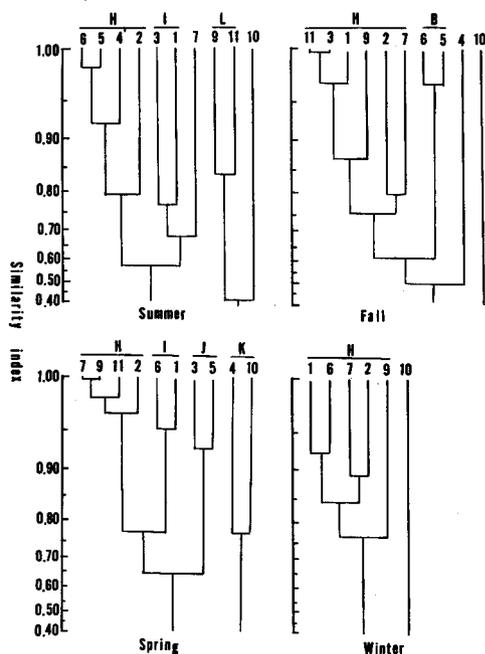


Fig. 27. Plot of results of the cluster analysis as a dendrogram for each sample collected in Lake Notoro-ko in 1978 after the mouth was artificially constructed.

H: *Mitrella* type community, I: *Mitrella-Prionospio* type community, J: *Mitrella-Pseudochironomus* type community, B: *Prionospio* type community, K: *Dorvillea* type community, L: *Cistenides* type community.

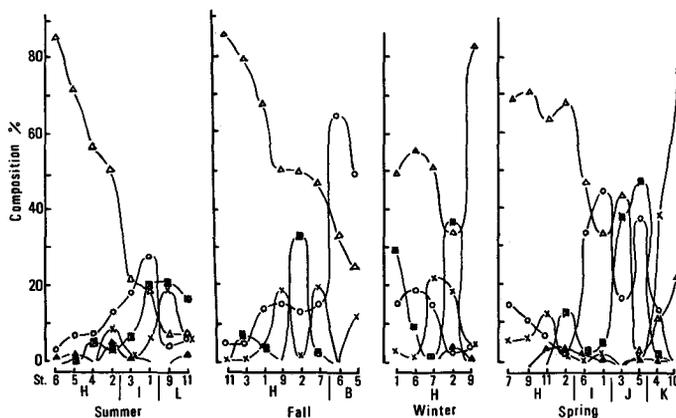


Fig. 28. Map showing the composition percentage of common species in each community in Lake Notoro-ko in 1978. See Fig. 27 for H-L and symbols as in Fig. 25.

other principal members in this community are common, on the whole, to those of *Mitrella* type community of Cluster group H (Fig. 28). These two communities, consequently, resemble each other showing a value of 0.6 in similarity (Fig. 27). This type occurs in the inner and the outer parts in seasons from spring to summer.

4) Cluster group J (*Mitrella-Pseudochironomus* type community). This is principally composed of *M. tenuis* and *Pseudochironomus* sp. showing 65–80% in percentage composition, and secondarily predominated by *P. malmgreni*. This community occurs only in spring in the shallow part in the central area, and is fairly similar to *Mitrella* type and *Mitrella-Prionospio* type showing a value higher than 0.65 in similarity index.

5) Cluster group K (*Dorvillea* type community). This is clearly distinguished from another communities described above in respects that *Dorvillea japonica* occurs in large numbers while *M. tenuis* is rare. This type appears only in spring in the deepest central part, formerly the azoic zone.

6) Cluster group L (*Cistenides-Dorvillea* type community). This is mainly composed of *C. soldatovi* and *D. japonica* with high composition percentage and secondarily predominated by one species of the pelecypods. This community occurs only in summer.

In 1978 in Notoro-ko *M. tenuis* is the highest species in abundance. Though there is some differences in species composition, large part of the lake is predominated on the whole by *M. tenuis* through the year round, and rather a good similarities are recognized between six cluster groups (Fig. 27). In short, communities are indistinct or discontinuous. This fact may prove that the seasonal changes in areal distribution and in species composition of communities show a tendency of simplification as compared with those in 1972 before the construction of the opening (Fig. 29).

(3) Hakodate Bay

The dendrograms are shown in Fig. 30 for the classification of communities by using the same procedure as that in the protected lake or lagoon described above.

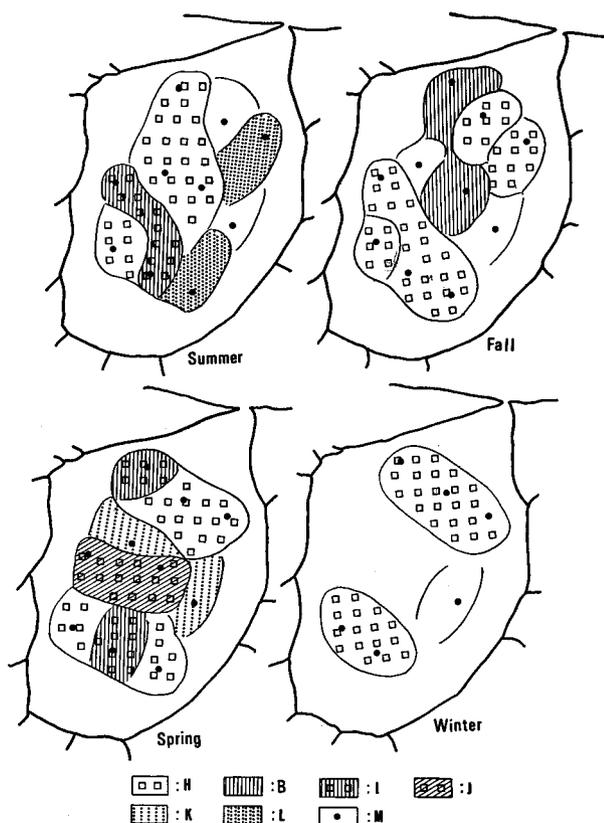


Fig. 29. Map showing the seasonal and spatial distributions of benthic communities in Lake Notoro-ko in 1978.

H: *Mitrella* type community, I: *Mitrella-Prionospio* type community, J: *Mitrella-Pseudochironomus* type community, B: *Prionospio* type community, K: *Dorvillea* type community, L: *Cistenides* type community, M: Samples which are devoid of similarity.

Six cluster groups are evident in the dendrogram in summer, five groups in fall, four in winter and three in spring, respectively. Calculations of mutual similarity indices among these communities result the following eight communities.

The distribution frequency of dominant species in each community are shown in Fig. 31, and areal and seasonal distributions in Fig. 32.

1) Cluster group A (*Chaetozone* type community). This is mainly predominated by *Chaetozone* sp. and secondarily by *Cirratulus cirratus*, *Lumbrineris* sp. and *Capitella capitata*, but polychaetes are few in occurrence. The distribution center of this community occupies the inner part of Hakodate Harbor in all seasons.

2) Cluster group B (*Chaetozone-Capitella* type community). This community is composed of, for the most part, the same members as those in *Chaetozone* type community, though *Chaetozone* sp. is few and composition percentage of *C.*

capitata is higher than that of *Chaetozone* type community. Species numbers of polychaetes also increase decidedly. This community occurs in the central part of the bay in summer and spring.

3) Cluster group C (*Chaetozone-Cirratulus-Capitella* type community). This is composed of the same principal members as those of *Chaetozone-Capitella* type community. Numbers of polychaetes is also same as in the latter community. This is highly correlated with it showing higher than 0.7 in an index value of similarity (Fig. 30). This community is distinctly distinguished from *Chaetozone-Capitella* type community with respect to the composition percentage of *C. cirratus*

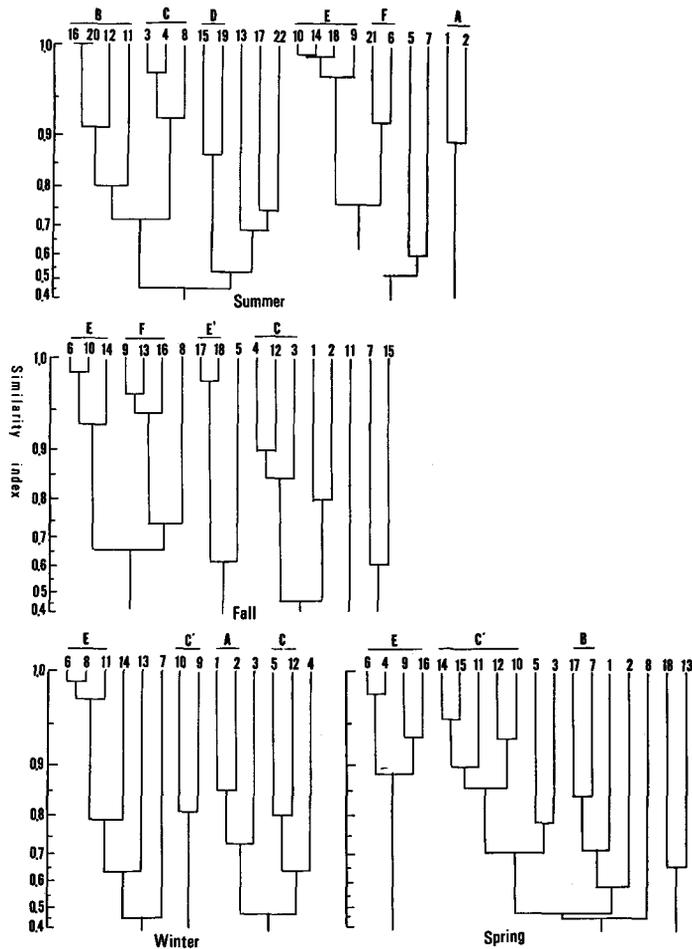


Fig. 30. Dendrogram based on cluster analysis of the samples collected in Hakodate Bay. A: *Chaetozone* type community, B: *Chaetozone-Capitella* type community, C: *Chaetozone-Cirratulus-Capitella* type community, C': *Chaetozone-Cirratulus-Mactra* type community, D: *Capitella-Gammarid C* type community, E: Gammarid A-B type community, E': Gammarid A-*Nephtys* type community, F: Gammarid A type community.

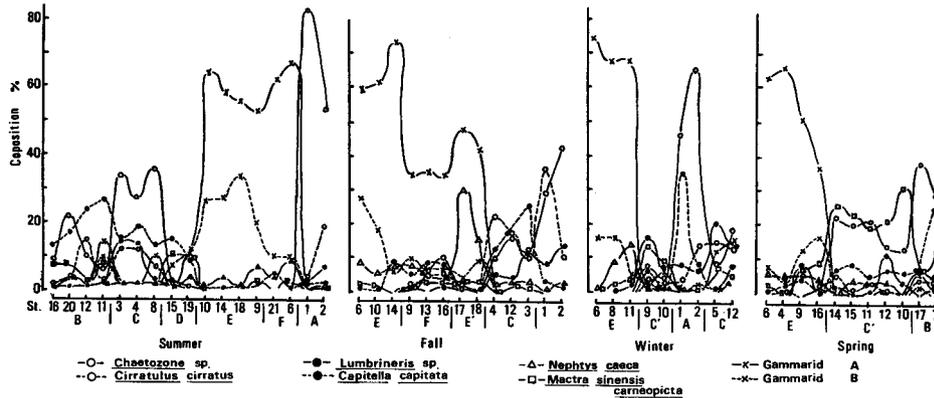


Fig. 31. Map showing the composition percentage of eight common animals in each community in Hakodate Bay. See Fig. 30 for A-F.

and *Chaetozone* sp. which are higher than those of *Chaetozone-Capitella* type community, and occurs in Hakodate Harbor and in the central part of the bay in all seasons except spring.

4) Cluster group C' (*Chaetozone-Cirratulus-Mactra* type community). This is somewhat correlated with *Chaetozone-Cirratulus-Capitella* type community. However, this differs from it in the increased number of individuals of the three pelecypods, *Mactra sinensis carneopicta*, *Yoldia excavata* and *Spisula sachalinensis*. This community occurs in seasons from winter to spring well coinciding with *Chaetozone-Capitella* type community and *Chaetozone-Cirratulus-Capitella* type community found from summer to fall, and its areal extent is especially spread in spring.

5) Cluster group D (*Capitella-Gammarid C* type community). This is distinguished from other communities observed in the area with respect to that *C. capitata* and Gammarid C are rather high in composition percentage, but that no dominant species with extremely large numbers are found. This community occurs only in summer in the outer area of the habitat of *Chaetozone-Capitella* type community.

6) Cluster group E (Gammarid A-B type community). This is predominated by various gammaridean members, especially by Gammarid A and Gammarid B. Polychaetes are few in species number. One of the polychaetes, *Nephtys caeca* is more or less abundant in number of individuals. This community is clearly distinguished from other communities described above and occurs near the shallow shores in all seasons.

7) Cluster group E' (Gammarid A-*Nephtys* type community). This is common to Gammarid A-B type community with respect to that Gammarid A and *N. caeca* are dominant species but is distinguished from it by the rarity of polychaetes in numbers of species and of individuals. This community occurs only in fall in the shallow waters neighboring the Gammarid A-B type community.

8) Cluster group F (Gammarid A type community). This is highly correlated with Gammarid A-B type community in a similarity index higher than 0.7, but differs from Gammarid A-B type in respect to rather high composition percentage

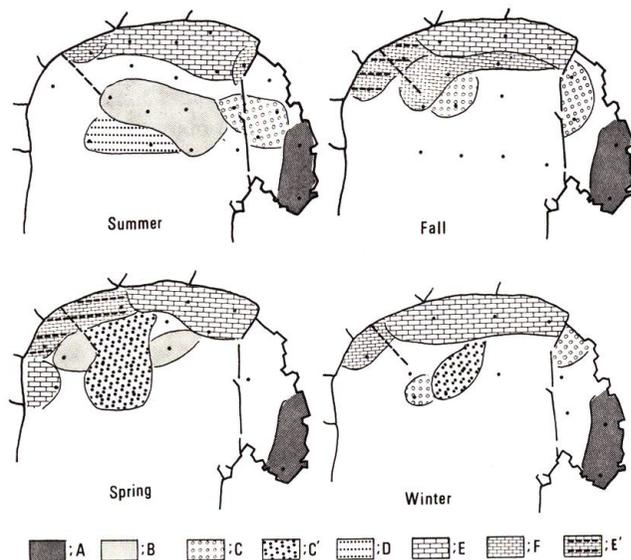


Fig. 32. Seasonal and spatial distributions of benthic communities in Hakodate Bay identified in Fig. 30. See Fig. 30 for A-F.

of Gammarid A and rather low percentage of Gammarid B, and moreover comparatively large number in species of polychaetes. This type develops in the area adjoining Gammarid A-B type community in seasons from summer to fall.

As is known from Fig. 32 showing distributions in time and space of communities in Hakodate Bay, various communities do not greatly change their areal distribution in all seasons. *Chaetozone* type community is found in the inner part in Hakodate Harbor. *Chaetozone-Cirratulus-Capitella* type community is found in the western area in the harbor and in the central part of the bay and Gammarid A-B type community is found near the shallow shores. Of three communities mentioned above, *Chaetozone-Cirratulus-Capitella* type community is partially replaced by *Chaetozone-Cirratulus-Mactra* type community only in spring.

Other four communities show more restricted distribution in time and space, and as can be seen in Fig. 32, *Chaetozone-Capitella* type community is found in the central part only in the seasons from spring to summer, Gammarid A type community on the shore only from summer to fall, *Capitella*-Gammarid C type community only in summer in the central part and Gammarid A-*Nephtys* type community only in fall near the shores.

3. Species diversities of benthic communities and changes in their seasonal distributions

Species diversity has two major components. One might be called the species richness component, as expressed by simple ratios between total species, S , and total numbers, N , and the other the species evenness in the apportionment of individuals among the species (Odum, 1961; Lloyd and Chelardi, 1964; Pielou, 1966). The diversity index that combines the richness and evenness components

tends to be low in physically controlled communities and high in biologically controlled communities (Odum, 1961; Sanders, 1968) or the low-diversity communities occur in highly predictable environments and the high-diversity communities in unpredictable environments (Huston, 1979). These facts may show that the structural changes of benthic communities caused by the changes of environment can be understood by the change of species diversity, and consequently it may be called one of the best indicators of an expression of the structural characteristics of benthic communities.

The different method of measuring diversity has been proposed by many workers up to now (Margalef, 1958; Morisita, 1961; Sanders, 1968; Ito, 1976; Kimoto, 1976). It has been employed according to the differences in the sense for diversity used or sample size collected.

In this paper is employed Shannon-Wiener information statistic which combines the richness and evenness and which is reasonably independent of sample size. The formula for calculating diversity is:

$$H' = - \sum_{i=1}^s \frac{n_i}{N} \log_2 \frac{n_i}{N}$$

Where n_i is the number of individuals of the i -th species and N the total number of individuals, and s is the total number of species.

(1) Zyusan-ko

Diversity indices of eight communities classified on the community type and differences in significance are tabulated in Table 9.

In August *Corbicula* type community (A) shows the lowest value in diversity indices and *Heteromastus*-Nemertinea type community (D) the highest. Diversities of *Corbicula* type community (A) and *Notomastus* type community (H) which show no significant differences between their means, are significantly lower than those of *Corbicula*-*Heteromastus* type community (C), *Heteromastus* type community (B) and *Heteromastus*-Nemertinea type community (D) which also show no significant differences to each other. In seasons from fall to spring, significance of difference between diversity indices of communities in every months may not be recognized except the diversity of *Corbicula* type community (A) in December which is significantly lower than that of *Prionospio*-*Heteromastus*-*Corbicula* type community (G) in the same month. Though the occurrence covers more than two seasons, *Corbicula* type community (A), *Corbicula*-*Heteromastus*-*Prionospio* type community (E) and *Prionospio*-*Heteromastus*-*Corbicula* type community (G) do not differ significantly in their respective diversities in various seasons as given in Table 9.

Structural characteristics of benthic communities in Zyusan-ko are summarized as follows from the viewpoint of species diversity: *Corbicula* type community in summer and winter distinctly shows the lowest diversity, whereas *Heteromastus*-Nemertinea type community in summer and *Prionospio*-*Heteromastus*-*Corbicula* type community in winter show diversity indices higher than those of other communities. In different seasons no significance of differences is observed in the diversities of one and the same community.

Table 9. Diversity H' (upper) of benthic communities in Lagoon Zyusan-ko and t-values (under) for difference between the average diversity H'. See Fig. 21 for A-H.

		Cluster group							
		A	B	C	D	E	F	G	H
Aug.	Diversity H'	0.41	1.69	1.61	1.95	—	—	—	1.09
	Standard error of mean	0.15	0.33	0.09	0.01	—	—	—	0.51
Oct.	Diversity H'	0.90	—	—	—	1.59	—	—	—
	Standard error of mean	0.65	—	—	—	0.09	—	—	—
Dec.	Diversity H'	0.47	—	—	—	—	—	1.52	—
	Standard error of mean	0.26	—	—	—	—	—	0.25	—
Apr.	Diversity H'	1.16	—	—	—	1.38	1.89	1.66	—
	Standard error of mean	0.62	—	—	—	0.05	0.07	0.15	—

	Aug.				Oct.		Dec.		Apr.			
	B	C	D	H	A	E	A	G	A	E	F	G
A	4.31*	7.30*	5.59*	1.32	1.05	11.0	2.48	4.12*	1.60	6.06*	9.76*	5.26*
B		0.30	0.91	1.14	1.23	0.40	2.89*	0.37	0.85	0.95	0.69	0.09
C			2.26*	1.80	1.68	0.09	4.71*	0.42	1.12	2.05	2.57*	0.28
D				3.01*	2.70*	2.56*	6.16*	1.90	2.11	3.81*	0.40	1.52
H					0.25	1.97	1.38	0.89	0.09	0.90	2.91*	1.74
A						2.00	2.36	2.73*	0.29	0.97	2.41	1.95
E							5.22	0.36	1.30	1.60	2.40*	0.40
A								2.72*	0.29	0.97	2.41	1.95
G									0.54	0.73	1.99	0.48
A										1.08	1.87	1.32
E											5.43*	1.28
F												1.18

* difference significant (P<0.05)

(2) Notoro-ko

In 1972 diversity of *Prionospio* type community (B) occurring in summer shows significantly lower than that of *Musculus-Ampelisca* type community (F) occurring in the same season and *Cistenides* type community (E) occurring in fall shows higher diversity than those of other communities in the same season. Diversity indices of communities occurring in winter and spring, however, show no significance of differences in various seasons (Table 10). *Musculus* type community (A), *Prionospio* type community (B) and *Pseudochironomus* type community (C) occurring during more than two seasons show no significant differences in their respective diversities between seasons. In conclusion, it is considered that in Notoro-ko in 1972 *Musculus-Ampelisca* type community occurring in summer and *Cistenides* type community occurring in fall show rather high diversity indices, whereas other communities are generally low diversity ones.

In 1978 diversity indices of *Mitrella* type community (H) show low values ranging 1.7-2.0 throughout the year round, and *Mitrella-Prionospio* type community

Table 10. Diversity H' (upper) of benthic communities in Lake Notoro-ko in 1972 before the mouth was artificially constructed and t-values (under) for difference between the average diversity H'. See Fig. 24 for A-G.

		Cluster group						
		A	B	C	D	E	F	G
Summer	Diversity H'	1.78	1.13	—	—	—	2.96	—
	Standard error of mean	0.43	0.17	—	—	—	0.03	—
Fall	Diversity H'	1.48	—	—	1.72	2.30	—	1.45
	Standard error of mean	0.34	—	—	0.35	0.10	—	0.15
Winter	Diversity H'	—	0.83	1.42	—	—	—	—
	Standard error of mean	—	0.18	0.23	—	—	—	—
Spring	Diversity H'	0.90	1.69	1.53	—	—	—	—
	Standard error of mean	0.28	0.28	0.39	—	—	—	—

	Summer		Fall				Winter		Spring		
	B	F	A	D	E	G	B	C	A	B	C
A	1.53	2.28	0.55	0.09	0.81	0.51	2.03	0.79	1.78	0.12	0.36
B		7.49*	0.92	1.74	4.08*	1.07	1.23	0.98	0.72	1.72	1.12
F			3.21*	3.31*	3.53*	7.27*	8.87*	4.43*	5.34*	4.67*	4.19*
A				0.47	1.45	0.06	1.56	0.14	1.32	0.36	0.08
D					1.24	0.59	2.47*	0.74	1.82	0.06	0.06
E						4.62*	5.31*	2.08	2.97*	2.05	1.90
G							2.15	0.05	1.15	0.77	0.19
B								1.86	0.20	2.40	1.95
C									1.46	0.61	0.22
A										1.48	1.22
B											0.34

* difference significant (P<0.05)

(I) occurring in spring and summer and *Dorvillea-Cistenides* type community (L) occurring only in summer show significantly high diversity indices (Table 11). In any case, when compared the diversity indices obtained in 1978 with those in 1972 as shown in Table 10 and Table 11, communities occurring in 1978 are characterized by exceedingly higher diversity indices. Judging from benthic communities collected in 1978 and 1972, they are presumed to change successively toward higher diversity.

(3) Hakodate Bay

Gammarid A-B type community (E) occurring in all seasons shows significantly the lowest diversity indices, and *Chaetozone* type community (A) and Gammarid A-*Nephtys* type community (E') denote rather low diversities, while *Chaetozone-Capitella* type community (B), *Chaetozone-Cirratulus-Capitella* type community (C), *Capitella*-Gammarid C type community (D) and *Chaetozone-Cirratulus-Mactra* type community (C') show significantly higher diversity indices respectively in every seasons of their occurrence (Table 12).

Table 11. Diversity H' (upper) of benthic communities in Lake Notoro-ko in 1978 after the mouth was artificially constructed and t-values (under) for difference between the average diversity H' . See Fig. 27 for H-L.

		Cluster group					
		H	B	I	J	K	L
Summer	Diversity H'	2.00	—	2.96	—	—	3.12
	Standard error of mean	0.18	—	0.06	—	—	0.04
Fall	Diversity H'	1.69	1.41	—	—	—	—
	Standard error of mean	0.18	0.35	—	—	—	—
Winter	Diversity H'	1.93	—	—	—	—	—
	Standard error of mean	0.18	—	—	—	—	—
Spring	Diversity H'	1.74	—	2.18	1.80	1.74	—
	Standard error of mean	0.04	—	0.24	0.09	0.97	—

	Summer		Fall		Winter	Spring			
	I	L	H	B	H	H	I	J	K
H	3.49*	4.09*	1.14	1.70	0.27	1.39	0.65	0.36	0.40
I		4.30	3.75*	4.37*	3.41*	16.20*	7.09	4.40*	1.26
L			4.23*	4.86*	3.95*	20.10*	9.69	5.16*	1.43
H				0.75	0.92	0.21	1.44	0.56	0.09
B					1.47	1.47	2.13	1.13	0.32
H						0.92	0.13	0.12	0.32
H							5.95*	0.95	0
I								1.15	0.45
J									0.15

* difference significant ($P < 0.05$)

In Hakodata Bay there may be two community groups as observed from a species diversity viewpoint. One such is the low-diversity communities with index values lower than 2.5 as Gammarid A-B type community, *Chaetozone* type community and Gammarid A-*Nephtys* type community and the other is the high-diversity communities with index values higher than 3.0, such as communities of *Chaetozone-Capitella* type, *Chaetozone-Cirratulus-Capitella* type, *Capitella*-Gammarid C type and *Chaetozone-Cirratulus-Mactra* type.

4. Discussion

To analyse the structural characteristics of benthic communities, since a relatively few species generally exert the major controlling influence by virtue of their numbers (Odum, 1961), seasonal and areal distributions of dominant species were investigated at first. Secondly, communities were classified on a basis of cluster groups obtained from the statistical comparisons by means of similarity indices. Finally, diversities of benthic communities were clarified.

Many classification techniques were proposed for the interpretation of community by many workers such as correlation-coefficient analysis (Motomura,

Table 12. Diversity H' (upper) of benthic communities in Hakodate Bay and t-values (under) for difference between the average diversity H'. See Fig. 30 for A-F.

		Cluster group								
		A	A'	B	C	C'	D	E	E'	F
Summer	Diversity H'	1.83	—	3.73	3.22	—	3.75	1.57	—	2.03
	Standard error of mean	0.57	—	0.04	0.10	—	0.11	0.07	—	0.17
Fall	Diversity H'	—	3.06	—	3.58	—	—	1.78	2.33	3.43
	Standard error of mean	—	0.09	—	0.06	—	—	0.14	0.07	0.05
Winter	Diversity H'	1.89	—	—	3.53	3.67	—	1.50	—	—
	Standard error of mean	0	—	—	0.02	0.03	—	0.11	—	—
Spring	Diversity H'	—	—	3.31	—	3.51	—	2.42	—	—
	Standard error of mean	—	—	0.13	—	0.06	—	0.24	—	—

	Summer					Fall					Winter				Spring		
	B	C	D	E	F	A'	C	E	E'	F	A	C	C'	E	B	C'	E
A	5.40*	3.15*	3.33*	0.72	0.34	2.15	4.08*	0.11	0.88	3.75*	0.11	3.01*	3.25*	0.74	2.55	5.29*	0.89
B		5.09	0.21	27.0*	14.0*	7.89*	2.00	15.3*	17.5*	4.41*	27.5*	2.96*	0.87	20.6*	4.01*	2.66*	5.39*
C			3.42*	14.2*	6.02*	1.10	3.00*	8.36*	6.29*	1.84	10.1*	2.36	3.38*	10.1*	0.55	2.56*	2.71*
D				1.81	34.3*	4.96*	1.47	10.0*	10.9*	3.02*	16.9*	2.07	0.70	13.4*	2.59	1.96	3.65*
E					3.24*	13.2*	21.2*	1.50	7.02*	20.8*	3.21*	19.6*	20.7*	0.57	13.6*	20.8*	3.43*
F						5.54*	10.4*	1.16	1.68	10.0*	0.85	9.04*	9.76*	2.87*	6.10*	10.7*	1.19
A'							5.04*	6.77*	6.64*	4.01*	13.7*	5.40*	6.78*	9.76*	1.61	3.87*	2.00
C								11.8*	12.9*	1.80	20.5*	0.61	1.06	16.1*	2.13	0.72	4.03*
E									2.97*	11.23*	0.62	9.83*	10.5*	1.57	7.55*	13.1*	2.09
E'										12.9*	6.29*	16.6*	17.6*	5.38*	6.62*	10.4*	0.69
F											23.1*	1.48	3.41*	13.9*	1.02	0.86	3.53*
A												10.2*	59.3*	11.2*	10.9*	15.1*	1.48
C													4.13*	13.9*	1.68	0.12	3.51*
C'														14.76*	2.71	1.48	3.95*
E															10.3*	17.0*	3.23*
E'																1.57	2.42
F																	4.91*

* difference significant (P<0.05)

1935; Yamamoto, 1950), percentage analysis (Kato et al., 1952; Yamamoto, 1955) and trellis diagram analysis (Wieser, 1960; Sanders, 1960). All of these techniques are based on similarity analyses for which many samples are taken in a given region and classified into composite groups of samples with high similarity. It may be impossible with these techniques to compare similarities objectively between groups. In the classification analysis employed in the present study, the samples are statistically and objectively divided into groups, and from the matrix a dendrogram is prepared which shows the relationships between sample groups.

As for the methods of measuring diversity, it is a drawback that the diversity index is controlled by the sample size, therefore it is not widely applicable (Morisita, 1961). The Shannon Wiener information statistic, H' index, employed in this study is one of the best methods to check the diversity index because it is reasonably independent of the sample size. It is also normally distributed (Bowman et al., 1970; Hutcheson, 1970), so the routine statistical methods can be used to test the significance of differences between means. Many studies treating diversities of benthic communities have so far reported differences of diversity indices only between stations sampled (Wilhm, 1967; Sanders, 1968), and the studies dealing with diversities statistically between benthic communities are few. As is evident from the comparison of community types and their diversities obtained in each area surveyed, such communities characterized by a single species with extremely high composition percentage as seen in communities of *Corbicula* type and *Notomastus* type in Zyusan-ko, *Musculus* type, *Prionospio* type and *Pseudochironomus* type in Notoro-ko in 1972 and *Mitrella* type, *Dorvillea* type and *Prionospio* type in the same lake in 1978, and also Gammarid A-B type and *Chaetozone* type in Hakodate Bay show distinct diversity indices lower than those of community types characterized by 2-5 species in respective area. This fact may demonstrate that all the organisms in the community are not equally important in the determination of the community structure (Odum, 1961), and that a few species with dense populations found in each area surveyed may greatly control the community structure (Holland and Polgar, 1976; Frankenberg and Leiper, 1977; Kikuchi and Tanaka, 1978; Nakao, 1979).

In the previous studies data of benthic community structure based on the species composition partly consisted of samples taken only in a single sampling period or in particular season (Yamamoto, 1950, 1955; Kosaka et al., 1972; Holland and Dean, 1977; Hayashi, 1978). Therefore, annual changes in areal and seasonal distributions of benthic communities have been known a very little. Seasonal variation has not been found in the soft bottom communities in Buzzards Bay, Massachusetts (Sanders, 1960), in Shimizu Harbor and Orido Bay, Shizuoka Prefecture (Kosaka et al., 1972) and on the coast of Seto Inland Sea (Kitamori, 1963). From these reports it may be safely stated that seasonal variations are rarely observed in the benthic community structure. On the contrary, a considerable number of investigations pointed out that seasonal changes in the community structure were clearly controlled by the fluctuations in the population densities of dominant species (Yamamoto, 1952; Nakao, 1976; Frankenberg and Leiper, 1977; Holland and Polgar, 1977). Furthermore, number of species and individuals and biomass increase from spring to summer, and decrease from summer to fall (Hori-koshi, 1955; Kikuchi, 1969), and Yamamoto (1952) reported that these values

attained a maximum from August to November, and a minimum from February to April. Holland et al. (1977) described that the total faunal depletion occurred during summer, an initial recolonization during early fall, a secondary one during late fall, and that growth and structural development occurred during winter and spring, reflecting the successful recruitment of four species reproduced in fall.

Since most of temperate-zone invertebrates are reproductively active only seasonally (Crocker, 1967; Olive, 1971), it is possible to hypothesize that the structure of benthic communities dominated in number by these organisms will vary seasonally, depending upon their recruitment and mortality trends.

Finally the seasonal changes in areal distributions of major communities in each area surveyed are concluded as follows (Fig. 33).

Zyusan-ko: Three community series are observed in the lagoon as investigated from community types and their diversities. The first one is *Corbicula* type community which occurs near the shore. It shows no seasonal changes in the species composition, and is characterized by dense population of *C. japonica*, but is low in diversity. The second one occurs in the areas from the shore to the central part. This is characterized by *H. similis* and *C. japonica* during whole seasons, and *P. japonicus* increase in number from fall to spring, showing comparatively high diversity. The third one occurs in the central part. It also occurs seasonally

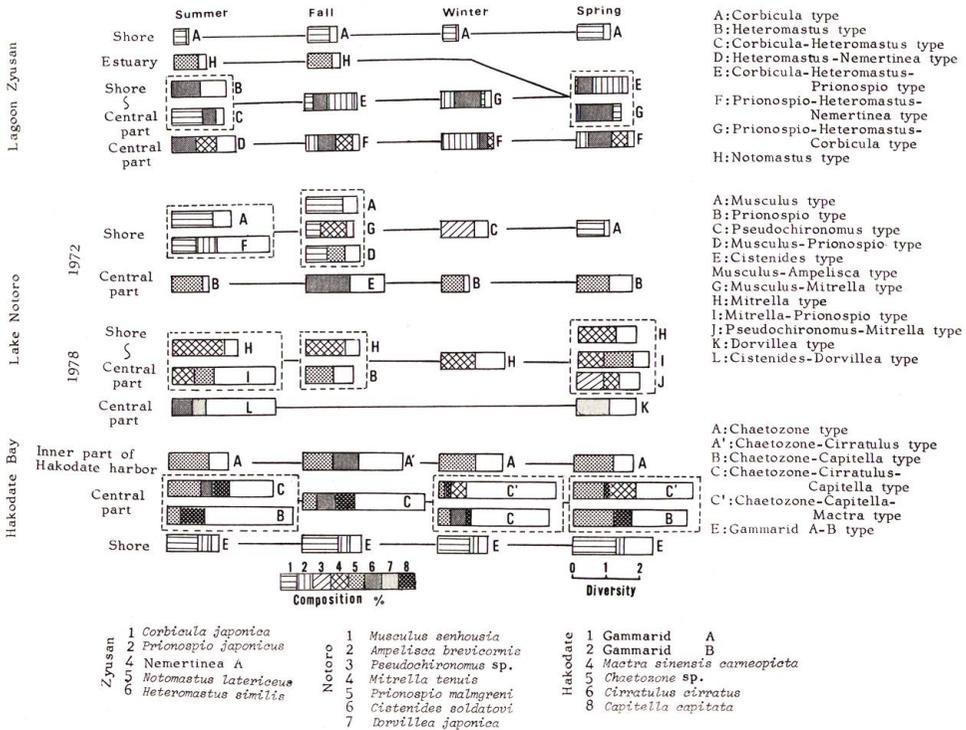


Fig. 33. Map showing the seasonal changes in the structure and ecological distributions of benthic communities in the surveyed areas.

predominated by *H. similis* and Nemertinea A all the year round, and *P. japonicus* from fall to spring, showing comparatively high diversity. Near the mouth of the Iwai River, *Notomastus* type community occurs from summer to fall showing low diversity and is alternated by the second community series from winter to spring with the recruitment of *P. japonicus*.

Notoro-ko: Two community series occur near the shore and in the central area as observed in both 1972 and 1978. There are, however, distinct differences between in communities in 1972 and 1978. In 1972, one occurs seasonally near the shore. It consists of *Musculus* type community, *Musculus-Ampelisca* type community and *Musculus-Mitrella* type community, which are relatively similar to each other, occurring from winter to summer, and *Pseudochironomus* type community occurs abundantly only in fall. The other series occurs in the central part encircling the azoic zone. It mainly consists of *Prionospio* type community throughout the year, although *P. malmgreni* is replaced by *C. soldatovi* only in fall. On the other hand, in 1978 community structures both near the shore and in the deep area show distinct differences as compared with those in 1972. The community series occurs widely in shallow regions from the shore to the center, consisting of similar community types, which are predominated by *M. tenuis* and one or two another species in every seasons. The distribution of the other community series coincides with that of azoic zone, and consists mainly of *D. japonica*.

Hakodate Bay: There are three community series as viewed from areal distribution and their diversities, of which two are not seasonal and an other one is seasonal in occurrence. The first one occurs in Hakodate Harbor mainly consisting of *Chaetozone* sp, in somewhat low diversities, and the second one occurs near the shore predominated by one or two species of gammarids in low diversities. Both of them are not seasonal in species composition and areal distribution. Whereas, the third one occurs in the central part of the bay consisting of four community types, of which structures are statistically similar to each other and characterized seasonally in high diversities. *Chaetozone* sp. is the most principal member among them, appearing in the whole seasons, and the appearance of *C. capitata*, *C. cirratus* and *M. sinensis carneopicta* is changed seasonally.

V. Relationships between benthic communities and environmental factors

To study the relationships between benthic communities and environment factors considerations must be paid on the three elements of environment, the quantity of ingestible food, the limits of tolerance of the organisms themselves to physical factors and the nature of the substrata where they live on or in, as described in Chapter III. There may be various cases in the relationships of organisms changing from a single factor of one element to several ones of one or more elements. In many of the previous investigations, however, those between the distributions of benthic communities and some environmental factors were commonly based on samples collected at a single sampling time (Yamamoto, 1951, 1954; Wigley and McIntyre, 1964; Kikuchi and Kikuchi, 1967; Nakao, 1969;

Johnson, 1970; Hayashi, 1978). This kind of information does not provide the scope necessary to determine if any real environmental influences are exerted on a community throughout its life span. Caution should be used when mapping benthic communities based on a single season's collection, since the aggregations may move seasonally into different habitats or be composed of different elements on a seasonal basis, as described in the previous chapter.

In this chapter are discussed the relations between distributions of benthic communities and their diversities and environmental factors basing on the changes in time and space in order to make clear the environmental influences on a benthic community.

If some real environmental influences are exerted on a benthic community structure, its characteristics can be widely used as an indicator of environmental conditions.

1. *Community types and environmental factors*

In the determination of the relationships between community types and environmental factors, the technique is usually employed comparing those distribution areas with the extent of environmental factors (Yamamoto, 1950, 1954; McIntyre, 1969; Hayashi, 1978).

Chlorinities in Hakodate Bay are extremely stable ranging from 18.64 ‰ in summer to 18.07 ‰ in winter, and oxygen contents are also stable ranging from 8.2 ml-O₂/l in winter to 6.0 ml-O₂/l in summer. Chlorinity and oxygen are therefore not considered as limiting factors in the composition and abundance of animals within the benthic communities in this region. It is also important to note that other elements of environment, nature of the substrata in relation to animal behaviors and quantity of ingestible food, may both be expected to affect composition and abundance in the region. Environmental factors in Zyusan-ko and in Notoro-ko fluctuate remarkably in time and space in a year, particularly, in chlorinities in bottom water in Zyusan-ko and in oxygen contents in bottom water in Notoro-ko. In addition, total sulfide contents in bottom sediment in Notoro-ko in 1972 show remarkably high values. Thus, these factors may have certain influences on the benthic communities in these respective regions.

(1) Hakodate Bay

The particle composition and the quantity of organic matter were determined to know the nature of the substratum and quantity of food in the environmental elements. Plotting the composition percentage of silt-clay fraction (larger than 4 ϕ in grain diameter) along the abscissa and carbon content in sediment (%) along the ordinate at every stations sampled, some station groups without duplication may be recognized as shown in Fig. 34.

The station group with low values of both silt-clay fraction and carbon content coincides with those of Gammarid A-B type (E) and Gammarid A-*Nephtys* type (E') communities. Of the station groups, the group with high values of carbon content coincides with that of *Chaetozone* type community (A) and the group with low carbon content does with that of *Chaetozone-Capitella* type community (B). Stations within Gammarid A type community (F) are located in the middle

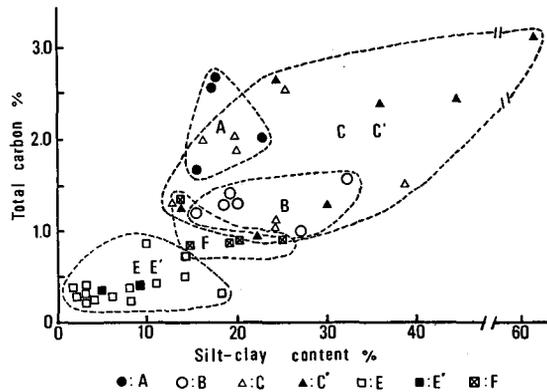


Fig. 34. Correlation between silt-clay content and total carbon content in sediment in Hakodate Bay. See Fig. 30 for A-F.

between Gammarid A-B type and *Chaetozone-Capitella* type. The station group with changeable values of them coincides with that of *Chaetozone-Cirratulus-Capitella* type (C) and *Chaetozone-Cirratulus-Mactra* type (C') communities.

When the relationships between community type and environmental element are observed on the basis of food supply, feeding mode of benthic animals within community and existent mode of food materials, such as deposit and suspension, should be considered at first. Since community type, therefore, is generally influenced by predominant members, ten predominant species in every stations are divided into carnivore, scavenger, suspension feeder, deposit feeder and surface deposit feeder after Dales (1962), Bloom et al. (1972), Santos and Simon (1974), Young and Young (1977) and Winter (1978) (Table 13). Then, benthos composition (%) based on feeding type, community type and carbon content (%) in sediment in every stations are shown in Table 14. Since communities in this region are extremely stable, only the results of May 1973 will be discussed here.

Gammarid A-B type community (E) consists mostly of suspension feeders with the composition percentage higher than 70%, while the composition of *Chaetozone-Capitella* type community (B) is generally composed of a few large deposit feeders with composition percentage higher than 60%, and *Chaetozone-Cirratulus-Mactra* type community (C) is composed of deposit feeders and surface deposit feeders with higher than 90% in composition percentage. Both of these latter communities consist rarely of suspension feeders with composition percentage lower than 10%. Furthermore, bottom sediments mainly occupied by suspension feeders show a rather small organic matter content (as total carbon content), and those occupied by deposit feeders and surface deposit feeders show more or less large organic matter content as shown in Table 14. As mentioned above, communities occurring in Hakodate Bay may be delimited by the particle composition and organic matter content in the sediment. This fact also may be proved by the relationships between feeding types of animals within communities and existent mode of ingestible food materials.

Table 13. List of common species with numbers of organisms

Species	Feeding type						
		1	2	3	4	5	6
<i>Nephtys caeca</i>	C	-	-	90	68	28	68
<i>Cirratulus cirratus</i>	D	107	141	62	11	39	-
<i>Cirriformia tentaculata</i>	D	22	-	-	-	-	-
<i>Magelona japonica</i>	D	5	28	-	-	-	-
<i>M. sp.</i>	D	-	11	34	-	113	-
<i>Lumbrineris sp.</i>	D	112	105	-	-	-	-
<i>Glycinde sp.</i>	C	1133	73	-	-	-	28
<i>Anaitides maculata</i>	C	11	-	-	17	-	28
<i>Chaetozone sp.</i>	D	136	85	73	-	85	-
<i>Laonice sp.</i>	SD	-	17	119	-	-	-
<i>Capitella capitata</i>	D	-	102	102	39	113	-
<i>Ophelia limacina</i>	D	11	-	-	51	-	17
<i>Prionospio krusadensis</i>	SD	-	-	-	-	56	-
<i>Chone sp.</i>	SF	-	17	39	-	-	-
<i>Maldane sarsi</i>	D	28	-	90	-	124	45
<i>Scoloplos armigera</i>	D	-	-	-	-	-	-
<i>Tharyx sp.</i>	D	-	-	-	-	-	-
Amphipoda	S	-	-	-	-	-	-
Pycnogonida	C	-	-	-	11	-	-
<i>Mactra sinensis carneopicta</i>	SD	-	175	345	17	170	22
<i>Spisula sachalinensis</i>	SD	-	-	-	-	68	-
<i>Yoldia johanni</i>	SD	-	-	-	-	-	22
<i>Patenopecten yessoensis</i>	SF	-	-	-	-	-	-
<i>Ophioplocus japonica</i>	D	-	-	-	-	-	-
Gammarid A	S, SF	-	17	192	927	68	710
B	S, SF	-	-	-	56	-	96
C	S, SF	-	-	-	126	-	-
D	S, SF	-	-	-	-	-	17
E	S, SF	-	-	-	56	-	-
Cumacea	S	-	-	-	11	-	-

C: carnivore, S: scavenger, SF: suspension feeder, D: deposit feeder, SD: surface deposit & Young (1977)

Table 14. Benthos composition (%) based on feeding type, community type
Community type

Feeding type	Community type							
	1	2	3	4	5	6	7	8
C	-	9.5	7.9	6.9	3.2	11.8	7.6	27.8
SF, S	-	2.2	16.8	84.6	7.9	78.2	-	10.1
S	0.7	2.2	3.4	-	-	-	2.7	-
D	98.6	61.2	31.5	7.3	54.9	5.9	72.7	11.4
SD	0.7	24.9	40.5	1.2	34.0	4.2	17.0	50.7
Community type	A	-	-	E	-	E	B	-
Total carbon (%)	2.1	1.4	1.3	0.2	0.8	0.3	1.4	1.1

1982]

NAKAO: Community structures of macro-benthos

found in 1 m² of sediment in Hakodate Bay in May 1973.

Station											
7	8	9	10	11	12	13	14	15	16	17	18
39	85	51	-	34	28	136	-	39	28	51	85
22	11	-	-	28	-	5	51	3	-	28	-
-	-	-	-	-	-	-	-	-	-	-	-
-	-	-	79	45	-	5	34	62	-	-	-
-	-	-	113	-	34	-	-	-	-	-	-
17	-	-	51	-	126	-	17	-	-	-	-
22	17	-	-	-	22	11	17	-	-	-	28
-	22	-	-	-	-	-	-	-	17	-	-
249	-	-	170	209	136	-	215	204	11	289	-
-	-	-	-	-	-	-	17	-	45	39	-
209	23	45	79	51	68	-	68	90	11	56	-
-	17	34	-	-	164	379	-	-	-	-	78
17	90	-	-	130	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-
-	-	11	-	28	-	-	-	-	-	-	-
-	-	-	-	-	28	-	22	-	-	-	-
51	-	-	-	45	-	-	-	45	-	-	-
5	-	-	39	-	-	-	-	34	-	-	-
-	-	-	39	-	198	-	-	34	-	-	-
102	102	68	396	198	-	11	249	232	68	45	51
17	-	-	62	68	28	-	73	73	-	-	5
-	34	68	-	-	-	136	17	34	73	28	232
22	-	-	34	39	22	-	22	28	-	-	-
34	-	-	-	-	-	5	56	-	-	22	-
-	34	427	-	-	-	217	-	-	262	46	58
-	-	111	-	-	-	66	-	-	125	-	10
-	-	-	-	-	-	-	-	-	-	37	-
-	-	7	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	17	-	-
-	11	11	-	-	-	28	-	-	-	-	5

feeder. Feeding types from Dales (1962), Bloom et al. (1972), Santos & Simon (1974), Young and Winter (1978).

and total carbon content in the sediment (%) in Hakodate Bay in May 1973.
as in Fig. 30.

Station									
9	10	11	12	13	14	15	16	17	18
6.1	3.7	3.9	5.9	14.7	2.0	8.3	6.8	8.0	20.7
66.7	3.7	-	-	31.1	-	3.9	61.5	12.9	13.3
-	3.2	4.6	-	-	2.6	3.2	-	-	-
10.8	46.3	46.4	48.5	39.4	54.0	45.8	3.3	61.6	13.3
16.3	43.1	45.3	45.7	14.7	41.5	38.7	28.3	17.5	52.7
E	C'	C'	C'	-	C'	C'	E	B	-
0.2	3.1	1.3	2.4	0.40	1.0	1.31	0.5	1.2	0.4

(2) Zyusan-ko

Of benthic animals occurring in Zyusan-ko, *C. japonica* (Asahina, 1941; Fuji, 1957; Yamamoto, 1959; Kikuchi, 1964), *N. japonica* (Beadle, 1937; Smith, 1955 a, b) and *P. japonica* (Okuda, 1953) are all able to tolerate the chlorinity variation by means of osmoregulatory abilities. Various workers reported that the distribution of mixohaline organisms are apparently regulated by chlorinity (Gunter, 1945; Remane and Schlieper, 1958; Welis, 1961). It is also reported that the optimum ranges of salinity for one species or community are often not for others (Asahina, 1941; Yamamoto, 1947; Kikuchi, 1976).

Chlorinities in bottom water in Zyusan-ko show the highest in summer and decrease distinctly from fall to winter and reach zero in spring in the whole area except near the opening. The seasonal changes in chlorinities as mentioned above externally correspond with the variation of population densities of *P. japonicus*, increasing from fall to spring, as is evident by comparing Figs. 11 and 17. No correspondence of this kind, however, can be found in other species. Since the seasonal and areal changes in the occurrence of communities in Zyusan-ko are clearly controlled by the fluctuation in population densities of *P. japonicus*, seasonal changes in the communities may consequentially and externally correspond with those of chlorinities. The communities in summer and their seasonal transformations between summer and fall are found in the same regions in every seasons of their occurrence (Fig. 23), and the areal extents of the communities do not expand or contract coincidentally with the chlorinity changes. Accordingly bottom water chlorinity may not be considered to be a limiting factor on the areal and temporal distributions of benthic communities.

Here, triangular graph paper is used to represent the percentage of three variables at every stations, such as silt-clay fraction, carbon content and interstitial chlorinity respectively extracted from three environmental elements as shown in Fig. 35. In summer in *Heteromastus*-Nemertinea type community (D) rather

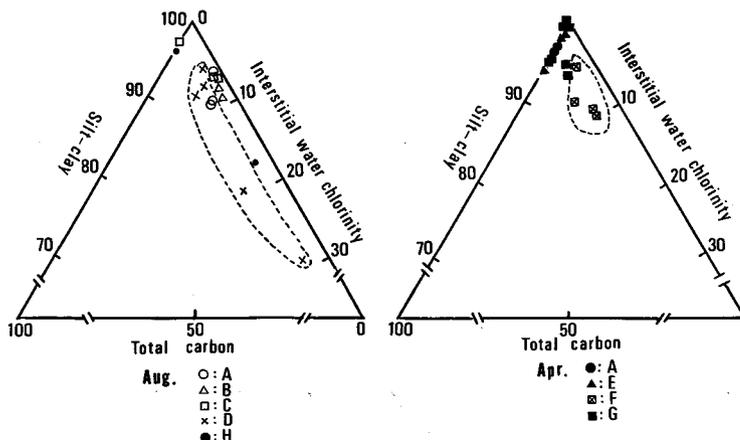


Fig. 35. Map showing the correlation among total carbon content, interstitial water chlorinity and silt-clay content in the sediment in Lagoon Zyusan-ko. See Fig. 21 for A-H.

high values and in another communities rather low values are seen in silt-clay fraction and interstitial chlorinity. In spring this tendency becomes clearer, that is to say, *Prionospio-Heteromastus-Nemertinea* type community (F) occupies the restricted region with rather high interstitial chlorinities, in exchange for *Heteromastus-Nemertinea* type community in summer.

Of the three benthic community series observed in Zyusan-ko, the first one including communities predominated by *H. similis* and *Nemertinea* A occurring in the whole seasons and *P. japonicus* occurring from fall to spring, shows rather high values in silt-clay fraction and interstitial chlorinity, and the other two series show rather low values.

Since carbon content is almost even in the areal extents of each series, it may not be considered as a limiting factor in the distribution of benthic communities in this lagoon.

(3) Notoro-ko

In 1972 Notoro-ko showed azoic nature in deeper region than 15 m all the year round as is classified into the permanent azoic lake in the classification of disharmonious lakes as described by Miyadi et al. (1950). This may be caused by a large amount of total sulfide in the sediment, resulted by the reduction of organic matter with deficient oxygen in summer. In fact, total sulfide in the sediments in the azoic zone indicates extremely high values in summer ranging from 1.3 to 10.1 ‰.

The construction of the opening in 1974 subsequently brings about a better aeration of the deep water, a rich amount of bottom oxygen content in all seasons and a complete disappearance of bottom oxygen deficiency found in summer (Figs. 14 and 15). Organic matter and total sulfide contents in the sediments in the deeper areas than 15 m except the central part decrease markedly with a disappearance of the oxygen deficient period mentioned above (Fig. 36).

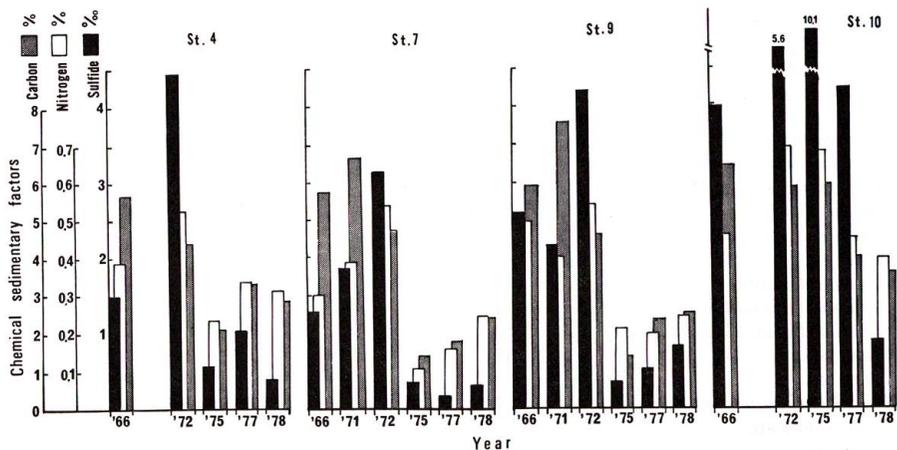


Fig. 36. Variations in the values of various chemical contents in the bottom sediment in which observed no appearance of macrobenthos till 1974.

Throughout the whole seasons in 1972 benthos are not observed on the regions deeper than 15 m with sediments having a large amount of total sulfide content (Sts. 4, 7, 9 and 10), but in 1975 a large number of species begins to occur except a comparatively small azoic zone around Station 10, and in 1977 only a few species occur also at Station 10 with total sulfide content, 4.24 ‰ (Table 15).

When the bottom oxygen content is not optimum for a species, the limit of tolerance may be reduced with respect to total sulfide content in the sediment. Azoic zone before 1974 is therefore formed in the area with total sulfide content

Table 15. Species name of benthic animals with numbers of individuals (no./m²) found during the summer sampling period in each year at Stations 4, 7, 9 and 10 situated in azoic zone in 1972 before the mouth was artificially constructed in Lake Notoro-ko.

Species name	Sept. 1975				Sept. 1977			
	St. 4	St. 7	St. 9	St. 10	St. 4	St. 7	St. 9	St. 10
<i>Mitrella tenuis</i>	-	3	-	-	6	1688	11	-
<i>Musculus senhousia</i>	31	85	119	-	23	170	136	-
<i>Mya arenaria oonogia</i>	-	-	-	-	6	-	-	-
<i>Harmothoe imbricata</i>	7	-	3	-	-	22	-	-
<i>Anatides maculata</i>	-	7	44	-	-	-	-	-
<i>Eteone longa</i>	14	3	17	-	-	-	11	-
<i>Stigambra tentaculata</i>	10	-	-	-	-	5	17	119
<i>Nereis zonata</i>	3	-	-	-	-	-	-	-
<i>Nephtys caeca</i>	-	-	-	-	-	-	5	-
<i>Glycinde</i> sp.	61	31	27	-	-	34	62	-
<i>Nothria</i> sp.	3	3	-	-	-	-	-	-
<i>Lumbrineris</i> sp.	-	31	-	-	-	130	5	-
<i>Dorvillea japonica</i>	459	10	7	-	527	153	209	10237
<i>Scolophos armiger</i>	7	10	3	-	-	-	-	-
<i>Laonice cirrata</i>	10	3	3	-	-	-	-	-
<i>Prionospio malmgreni</i>	116	88	34	-	-	357	436	-
<i>Spio</i> sp.	-	-	-	-	-	5	-	-
<i>Spiophanes bombyx</i>	-	-	-	-	-	-	22	-
<i>Pseudopolydora kempii japonica</i>	3	17	17	-	-	5	-	-
<i>Cirratulus cirratus</i>	-	-	-	-	-	39	5	-
<i>Pherusa plumosa</i>	3	-	-	-	-	-	10	-
<i>Scalibregma inflatum</i>	717	150	150	-	-	-	17	-
<i>Ophelia limacina</i>	-	3	-	-	-	-	-	-
<i>Heteromastus giganteus</i>	-	-	-	-	-	85	34	-
<i>Owenia fusiformis</i>	10	10	7	-	-	-	-	-
<i>Cistenides soldatovi</i>	-	-	3	-	-	102	-	-
<i>Pista</i> sp.	-	-	-	-	-	-	10	-
<i>Ampharete arctica</i>	-	-	3	-	-	-	-	-
<i>Mellinna elisabethae</i>	20	17	3	-	-	10	17	-
<i>Pseudosabellides littoralis</i>	7	3	-	-	6	5	5	-
<i>Chone</i> sp.	-	17	10	-	-	-	-	-
Cumacea	-	-	3	-	-	-	-	-
<i>Pseudochironomus</i> sp.	-	7	-	-	-	-	-	-
<i>Paranthura</i> sp.	-	-	-	-	-	5	-	-
Caprellidea	-	-	-	-	-	62	28	-
<i>Amphioplus ancistrotus</i>	3	-	-	-	-	158	5	-
Nemertinea	17	17	7	-	-	39	56	51

lower than 4%. After 1975 when bottom oxygen condition become favorable for organisms, about 4% in sulfide value may be the minimum amount of sulfide to form the azoic zone in Notoro-ko.

As stated already, in Notoro-ko before 1974 it may be inferred that bottom oxygen deficiency found in summer and extreme high total sulfide caused by both the former and a large amount of organic matter, are considered to be the two limiting factors concerning the occurrence of benthos.

To determine the relationships between community types and three environmental elements, three variables such as silt-clay fraction, carbon and total sulfide contents in the sediment are given in Fig. 37.

Of two community series in Notoro-ko in 1972, one occurs in the area with a comparatively high value in total sulfide as seen in the distribution of *Prionospio* type community in Fig. 37, and the other with a comparatively low value as seen in the distributions of *Musculus* type and *Musculus-Ampelisca* type communities in the same figure. Silt-clay fraction and carbon content are variety in those values, it can be therefore inferred that those are not considered to be limiting factors concerning the distribution of benthic communities in Notoro-ko.

2. Species diversities and environmental factors

Species diversities in benthic communities indicate generally high in Hakodate Bay and low in Zyusan-ko and in Notoro-ko in 1972. They differ, however, significantly in various communities in every regions surveyed. Determining, therefore, the relationships between benthic communities and environmental factors, it may be necessary to determine if any real environmental influences are exerted on a species diversity.

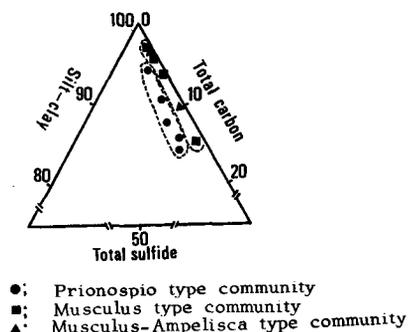


Fig. 37. Map showing the correlation among total sulfide content, total carbon content and silt-clay content in the sediment in Lake Notoro-ko in August 1972.

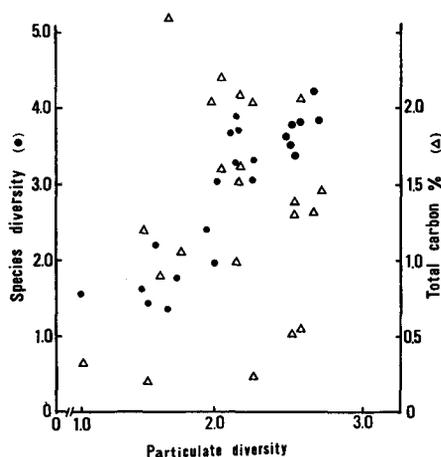


Fig. 38. Relations between particulate diversity and species diversity (●) and total carbon content (Δ) in Hakodate Bay.

(1) Hakodate Bay

Areal distribution of communities in Hakodate Bay were proved to be correlated with silt-clay fraction and organic matter content in the sediment preferred by each community, and this relationship was already explained by the feeding type of organisms within benthic community and the quantity of ingestible food.

Several authors have suggested that sediment heterogeneity or food diversity may influence shallow water infaunal species diversity (Gray, 1974; Johnson, 1974; Whitlatch, 1981). One of the problems in examining the influence of habitat and/or food complexity on infaunal and epifaunal species diversity appears to center around the devising of a meaningful measure of complexity. Gray (1974) and Nakao (1977), for instance, suggested that the sediment sorting coefficient may give some indications of grain-size variety. Whitlatch (1981), however, demonstrated that no correlation between sediment sorting and species diversity exist.

In order to assess what significance the variety of particulate food types and sediment complexity have on variations in benthic species diversity, particulate diversity (using the information index $H' = -\sum p_i \log_2 p_i$; Pielou, 1966) is estimated from surface sediment samples collected at each station.

Particulate categories used in the diversity calculation include seven grain-size fractions obtained from sieving. The relationships between particulate diversity indices and organic matter content and species diversity indices are shown in Fig. 38. As is evident from it, no correlation between particulate diversity and organic matter content is found, while a clear correlation between particulate diversity and species diversity does exist.

Particulate diversity in high values may show a high degree of sediment complexity, therefore, possibly many benthos species with various modes of living will occur. Since particle composition in sediment is influenced by the bottom current which may control food type (Sanders, 1958), particulate diversity also may indicate a variety of types of food ingested by benthic organisms with various feeding types.

(2) Zyusan-ko

In Zyusan-ko species diversities of benthic communities consisting of only a few species generally show indices lower than those in other regions investigated. It is natural because an organism must have osmoregulatory ability for its occurrence in such a poikilohaline lake with extreme chlorinity fluctuation as Zyusan-ko (Kinne, 1964, 1967). Nevertheless, communities in this lagoon consist of community types with a rather high species diversity and with a rather low one, and their distributions are found to be correlated with interstitial chlorinity gradient. From this fact, it is considered that a stable interstitial chlorinity in time and space may be a major limiting factor on the benthic species diversity, and their relation as observed in each station in spring and summer is shown in Fig. 39.

In spring and summer, samples collected in the area with interstitial chlorinities higher than 20 mg-Cl/g always show high diversity indices and samples lower than 20 mg-Cl/g, low diversity indices. It may be inferred that stable interstitial chlorinity may neutralize the influence of unstable bottom chlorinity which control the species diversity of benthic community.

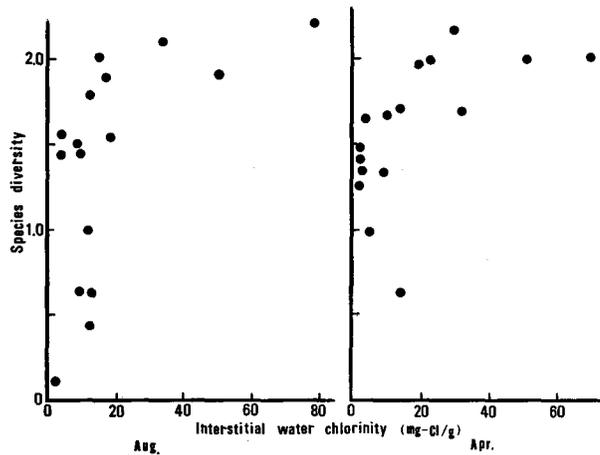


Fig. 39. Relationships between interstitial water chlorinity and species diversity H' in Lagoon Zyusan-ko.

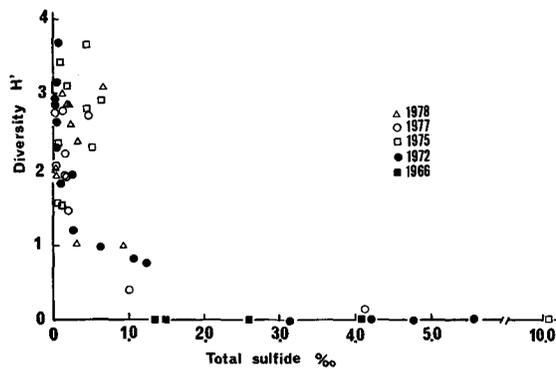


Fig. 40. Relationships between total sulfide content and species diversity H' in Lake Notoro-ko in Augusts 1966 to 1978.

(3) Notoro-ko

In the disharmonious lake such as Notoro-ko which has permanent azoic zone, environmental factors which benthos are limited in their occurrence seem to influence the species diversity of benthic community (Sanders, 1968). The relationship between species diversity indices at various stations sampled in summers from 1966 to 1978 and total sulfide in the sediment is shown in Fig. 40. Results obtained from the materials sampled in 1966 and 1972 show that diversity indices decrease markedly with increase of total sulfide, and abruptly fall below 1.0 in index value above 1.0 ‰ in total sulfide.

Species diversity indices obtained from the samples which are taken after the construction of the mouth also indicate a similar tendency. Those values show extremely low when total sulfide content exceeds 1.0 ‰. Though the values fluctuate considerably when total sulfide shows under 0.5 ‰, they tend to show higher values as compared with those of samples collected before the construction

of the mouth. Total sulfide such as 1‰ in value may strongly influence on the species diversity.

3. Discussion

For life, the external world which surrounds it is the environment (Shibuya, 1974) and the environment consists of various elements. Certain factors contained in these elements may provoke special influences on certain life. The environment may be connected with the life history of benthos that organize the benthic community. Therefore the environment also may be correlated to structural characteristics of benthic community.

To determine if any real environmental influences are exerted on a community type or on a species diversity obtained as a structural characteristic of benthic community will be indispensable for the determination of the role of benthic community in the benthic domain or for the application of benthic community as an indicator of the environment.

Caution should be paid when mapping benthic communities based on a single season's collection, since the aggregations may move seasonally into different habitats or be composed of different elements on a seasonal basis.

Not all elements in the environment are equally important in determining the relationships between community and environment. A relatively few elements generally exert the major controlling influence on the benthic community in each region surveyed.

Benthic communities in Hakodate Bay are found to be correlated with sediment particle composition, especially with silt-clay fraction. This relationship is biologically interpreted from a view point of feeding type of benthos and ingestible food supply. A hydrodynamic factor may influence both sediment particle compositions and food supply, that is to say, particulate organic matter as food of benthic organisms may be deposited on the sediment surface on the muddy bottom which has a weak bottom current, but may be suspended near the sediment surface on the sandy bottom which has a relatively strong bottom current. Muddy communities are therefore predominated by deposit feeders and sandy communities by suspension feeders (Sanders, 1958).

This fact stated above is also clearly understood from the relation between community and sediment particle composition in Hakodate Bay. *Chaetozone* type and *Chaetozone-Cirratulus-Mactra* type communities characterized by deposit feeders occur on the bottom which has high organic content in the sediment, but Gammarid A-B type and Gammarid A type communities characterized by suspension feeders occur on the bottom which has low organic content.

If a particulate diversity correlated with species diversity indicates habitat complexity and food variety, since an extremely strong current or a very weak current may cause particle size-fraction homogeneity and also reduce food variety, particulate diversities in those habitats will be commonly reduced. Therefore, two regions with the two extremes of bottom current will be respectively occupied by communities with similar low diversity indices. *Chaetozone* type community and Gammarid A-B type one are the exact examples of this information.

Among various environmental factors, chlorinity is found to be correlated

to benthic community in the mixohaline lake such as Zyusan-ko. The Venice System classification of brackish water, particularly the designation of euhaline, polyhaline, mesohaline and oligohaline, has been widely used to relate these schemes to the distribution of benthic community patterns. Kelley (1966) and Tenore (1972) reported that clear correlations exist between them. Boesch (1977) concluded, however, that benthic communities show no correlations between benthic community patterns and chlorinity designation schemes such as the Venice System, and that the distributions of estuarine organisms appear to be regulated by the boundary conditions of the minimum salinity throughout the annual cycle rather than by average conditions or a single season's condition.

Bottom chlorinities in Zyusan-ko are extremely unstable fluctuating between 15 ‰-Cl in summer and almost 0 ‰-Cl in spring. Areal distributions of benthic communities are considered to be controlled by stable interstitial chlorinities, not by bottom chlorinities. This can be easily understood from the fact that *C. japonica* with an osmoregulatory ability may reduce the stress of the unstable bottom chlorinity by the stable interstitial chlorinity as pointed out by Fuji in 1957.

Species diversity in the poikilohaline lake such as Zyusan-ko is distinctly influenced by the interstitial chlorinity. It may especially depend on the osmoregulatory ability of benthos against lower interstitial chlorinity.

High total sulfide content in the sediment in Notoro-ko is the major controlling factor of the benthic community. The value as 1.0 ‰ sharply reduces species diversity. Yoshimura et al. (1938) and Seisi et al. (1942) referred this value to tolerance limit of benthic organisms in Hamana-ko. In Notoro-ko when total sulfide in the sediment decreased as low as 4 ‰, the azoic zone turned into the biotic zone. Therefore the value 1.0 ‰ in total sulfide content may not be common tolerance limit of benthos. Needless to say, every benthic organisms have their resistance to H_2S (Jacubowa and Malm, 1931) and the resistance is influenced by coexistent water temperature or oxygen content (Theede et al., 1968).

As described above all the environmental elements are not equally important in determining the relationships between structural characteristics of benthic community and the environment. A major factor influencing the benthic community is the unique one which is variable in regions. This may indicate that the unique environmental factors are reflected by the benthic community structure. Hence structural characteristics of benthic community can be used as indicators of the environment.

VI. Experimental application of the benthic community to the evaluation of shellfish bed

Thorson (1955a, b, 1957) emphasized that communities of which the most important species are composed of the same genera or very closely related species are similar to each other not only functionally but also structurally. In the present paper it is demonstrated that the community type and species diversity have a correlation with environmental elements and that those characteristics of community structure depend mainly upon special species which have dense population. The results obtained from the above demonstration may suggest that shellfish beds of a

particular pelecypod, even if they are geographically isolated, may have similar communities in structure.

In this chapter principal components and species diversities of benthic communities observed in shellfish beds are compared with those in other areas. Then communities in various shellfish beds which are composed of a particular pelecypod will be unified basing on community types, principal components and species diversities. Finally it will be examined if those characteristics of communities unified can be used to the evaluation of the shellfish bed.

1. Communities in the shellfish beds

(1) Ezo giant scallop beds

In Fig. 41 are shown the areal distributions of scallop population sampled by a dredge and of macrobenthic communities sampled by Tamura grab sampler in Hakodate Bay and Lagoon Saroma-ko.

In Saroma-ko, of five community types which are structurally dissimilar to each other, *Lumbrineris* type community predominated by *Lumbrineris longifolia* shows the large areal extent. Its extent coincides with that of scallop with a dense population. Whereas in Hakodate Bay areal extents of *Chaetozone-Capitella* type and *Chaetozone-Cirratulus-Capitella* type communities coincide with that of scallop.

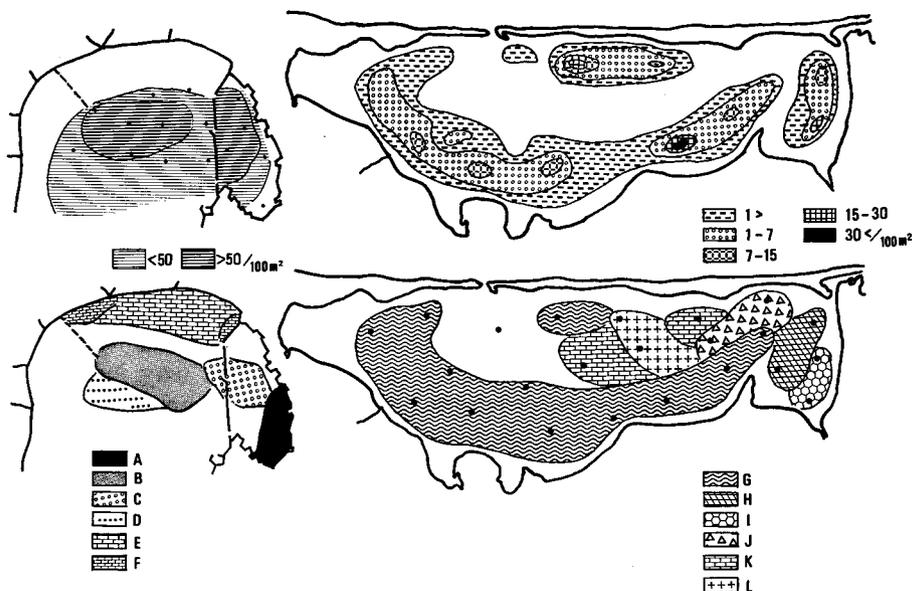
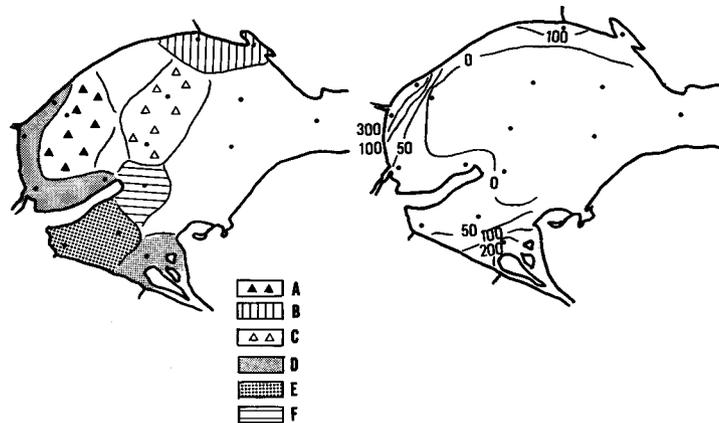


Fig. 41. Distributions of scallop population densities (no./100 m²) (upper) and of benthic communities (under) in August in Hakodate Bay (left) and in Lake Saroma-ko (right). A: *Chaetozone* type community, B: *Chaetozone-Capitella* type community, C: *Chaetozone-Cirratulus-Capitella* type community, D: *Capitella*-Gammarid C type community, E: Gammarid A-B type community, F: Gammarid A type community, G: *Lumbrineris* type community, H: *Spio* type community, I: *Dodecaceria-Scalibregma* type community, J: *Dodecaceria* type community, K: *Chaetozone-Sigambra* type community, L: *Sigambra* type community.

Table 16. Composition percentage (%) of common benthic fauna and diversity H' of communities found in scallop beds.

Hakodate Bay				Lake Saroma-ko	
<i>Chaetozone-Capitella</i> type community		<i>Chaetozone-Cirratulus- Capitella</i> type community		<i>Lumbrineris</i> type community	
<i>Capitella capitata</i>	20.0	<i>Chaetozone</i> sp.	32.3	<i>Lumbrineris longifolia</i>	35.6
<i>Chaetozone</i> sp.	12.3	<i>Capitella capitata</i>	15.7	<i>Dodecaceria concharum</i>	28.3
<i>Cirratulus cirratus</i>	6.0	<i>Cirratulus cirratus</i>	10.3	<i>Maldane sarsi</i>	11.2
<i>Mactra</i> sp.	5.3	<i>Lumbrineris</i> sp.	10.0	<i>Notomastus</i> spp.	8.5
Maldanidae	3.2	Gammarid sp.	2.3	<i>Sigambra tentaculata</i>	4.3
<i>Goniada</i> sp.	2.1	<i>Mactra</i> sp.	1.2	<i>Macoma</i> sp.	4.1
				<i>Goniada maculata</i>	4.0
Diversity H'	3.73		3.22		3.43

Fig. 42. Distributions of *Corbicular japonica* population densities (no./m²) (right) and of benthic communities (left) in Lagoon Furen-ko. A: *Macoma* type community, B: *Capitella* type community, C: *Nereis-Nainereis* type community, D: *Corbicula* type community, E: *Nereis-Corbicula* type community, F: *Prionospio* type community.

Composition percentage of five principal components in the scallop habitat and mean diversity indices, H' are shown in Table 16.

Many genera are common to two scallop habitats. For instance, both raise species of *Lumbrineris*, *Maldane* and *Goniada*. Furthermore, *Chaetozone* sp., *Cirratulus cirratus* occurring in Hakodate Bay and *Dodecaceria concharum* occurring in Saroma-ko, and *Capitella capitata* occurring in the former and *Notomastus* sp. occurring in the latter are very closely related species belonging to the same family. Both also show commonly high diversity indices.

(2) Freshwater clam beds

In Fig. 42 are shown the areal distributions of freshwater clam population and benthic communities observed in Lagoon Furen-ko in August 1979.

Table 17. Composition percentage (%) of common benthos and diversity H' of communities found in freshwater clam beds.

Lagoon Zyusan-ko					
<i>Corbicula</i> type community		<i>Heteromastus</i> type community		<i>Corbicula-Heteromastus</i> type community	
<i>Corbicula japonica</i>	96.9	<i>Heteromastus similis</i>	68.5	<i>Corbicula japonica</i>	45.9
<i>Heteromastus similis</i>	2.2	<i>Prionospio japonicus</i>	8.4	<i>Heteromastus similis</i>	29.0
<i>Nereis japonica</i>	0.4	<i>Corbicula japonica</i>	7.6	Nemertinea sp.	11.0
Nemertinea sp.	0.4	<i>Cyathura muromiensis</i>	6.3	<i>Prionospio japonicus</i>	6.6
		<i>Nereis japonica</i>	3.5	<i>Cyathura muromiensis</i>	5.5
				<i>Nereis japonica</i>	2.2
Diversity H'	0.41		1.69		1.61

Lagoon Furen-ko			
<i>Corbicula</i> type community		<i>Corbicula-Nereis</i> type community	
Small gastropod	32.1	<i>Nereis japonica</i>	43.8
<i>Corbicula japonica</i>	25.0	<i>Corbicula japonica</i>	28.2
<i>Macoma incongrua</i>	14.0	Capitellidae	18.7
<i>Eteone longa</i>	11.5	<i>Macoma incongrua</i>	16.0
<i>Nereis japonica</i>	9.8	<i>Eteone longa</i>	5.3
Capitellidae	7.4	<i>Prionospio malmgreni</i>	3.4
Diversity H'	1.98		2.13

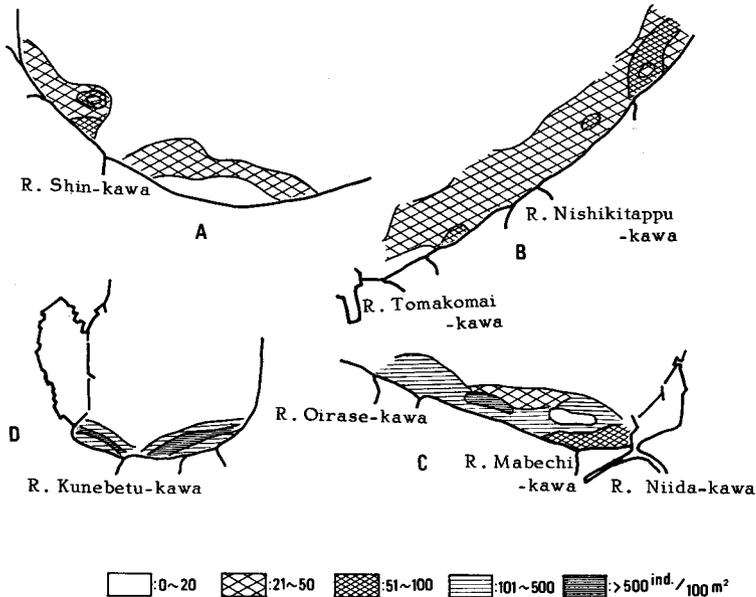


Fig. 43. Geographic distributions of number of individuals of surf clam per 100 m². A: Ishikari Bay. B: Coast along Tomakomai, C: Coast along Hachinohe, D: Hakodate Bay

Two similar communities are seen in its habitat, and similarity index shows 0.65 as measured by Mountford method. Composition percentage of the dominant species and their mean species diversities are given in Table 17. As is evident from a comparison of these two communities with three other communities which showed a good similarity in Zyusan-ko in August (Fig. 21), in freshwater clam beds are seen the same genera or very closely related species except small sized gastropod, *Macoma incongrua* and *Eteone longa* in Furen-ko. Diversities of these communities show commonly lower indices as seen in Table 17.

(3) Surf clam beds

In Fig. 43 are shown the areal distributions of surf clam population in Ishikari Bay and Hakodate Bay and on the coast of Tomakomai which were surveyed in summer of 1972, and on the coast along Hachinohe in summer of 1966.

Qualitative sampling of surf clam was carried out by means of a surf clam dredge except in Hakodate Bay where the quadrat method was employed. The towing speed was different for each respective place. Therefore, it may be impossible to compare directly the population densities in various habitats. However, four surf clam beds show common population densities of at least more than 20 to 50 individuals per 100 square meters.

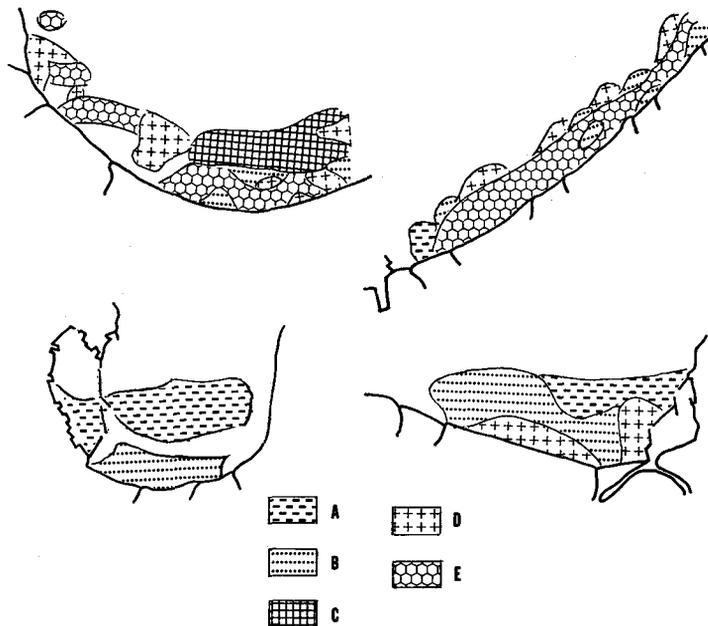


Fig. 44. Geographic distributions of five benthic communities in surf clam beds and adjacent waters of them.

A: Polychaete type community B: Gammarid or Crustacea type community C: *Echinocardium* type community D: Pelecypod type community E: *Scaphechinus* type community

Table 18. Common species and diversity H' of communities found in surf clam beds (upper) and neighboring area (under).

Ishikari Bay	Tomakomai Coast	Hakodate Bay	Hachinohe Coast
<p>Pelecypod type community</p> <p>1 <i>Tellina venulosa</i></p> <p>2 <i>Spisula sachalinensis</i></p> <p>3 <i>Mactra sinensis carneopicta</i></p> <p>4 <i>Nephtys caeca</i></p> <p>5 <i>Scaphechinus mirabilis</i></p> <p>Diversity H' 1.60</p> <p>Scaphechinus type community</p> <p>1 <i>Scaphechinus mirabilis</i></p> <p>2 <i>Tellina venulosa</i></p> <p>3 <i>Nephtys caeca</i></p> <p>4 <i>Mactra sinensis carneopicta</i></p> <p>5 <i>Spisula sachalinensis</i></p> <p>Diversity H' 1.34</p> <p>Gammarid type community</p> <p>1 Gammarids</p> <p>2 <i>Nephtys caeca</i></p> <p>3 <i>Mactra sinensis carneopicta</i></p> <p>Diversity H' 1.73</p> <p><i>Echinocardium</i> type community</p> <p>1 <i>Echinocardium cordatum</i></p> <p>2 <i>Tellina venulosa</i></p> <p>3 <i>Nephtys caeca</i></p> <p>Diversity H' 2.43</p>	<p>Pelecypod type community</p> <p>1 <i>Mactra sinebsis carneopicta</i></p> <p>2 <i>Nephtys caeca</i></p> <p>3 Gammarid sp.</p> <p>Diversity H' 1.05</p> <p>Scaphechinus type community</p> <p>1 <i>Scaphechinus mirabilis</i></p> <p>2 <i>Mactra sinensis carneopicta</i></p> <p>3 <i>Nephtys caeca</i></p> <p>4 <i>Tellina venulosa</i></p> <p>Diversity H' 1.65</p> <p>Crustacea type community</p> <p>1 <i>Tecticeps japonicus</i></p> <p>2 Gammarid sp.</p> <p>3 <i>Scaphechinus mirabilis</i></p> <p>4 <i>Tellina venulosa</i></p> <p>5 <i>Mactra sinensis carneopicta</i></p> <p>Diversity H' 1.76</p> <p>Polychaete type community</p> <p>1 Cirratulidae</p> <p>2 <i>Chirori</i> sp.</p> <p>3 <i>Nephtys caeca</i></p> <p>Diversity H' 2.09</p>	<p>Gammarid A-B type community</p> <p>1 Gammarid A</p> <p>2 Gammarid B</p> <p>3 <i>Nephtys caeca</i></p> <p>4 <i>Mactra sinensis carneopicta</i></p> <p>5 <i>Spisula sachalinensis</i></p> <p>Diversity H' 1.57</p> <p>Chaetozone-Capitella type community</p> <p>1 <i>Capitella capitata</i></p> <p>2 <i>Chaetozone</i> sp.</p> <p>3 <i>Cirratulus cirratus</i></p> <p>4 <i>Mactra sinensis carneopicta</i></p> <p>5 Maldanidae</p> <p>Diversity H' 3.73</p> <p>Chaetozone-Cirratulus-Capitella type community</p> <p>1 <i>Chaetozone</i> sp.</p> <p>2 <i>Capitella capitata</i></p> <p>3 <i>Cirratulus cirratus</i></p> <p>4 <i>Lumbrineris</i> sp.</p> <p>5 Gammarid sp. C</p> <p>Diversity H' 3.22</p>	<p>Pelecypod type community</p> <p>1 <i>Spisula sachalinensis</i></p> <p>2 <i>Mactra sinensis carneopicta</i></p> <p>3 <i>Scaphechinus mirabilis</i></p> <p>4 <i>Nephtys caeca</i></p> <p>Diversity H' 1.68</p> <p>Gammarid type community</p> <p>1 Gammarids</p> <p>2 <i>Mactra sinensis carneopicta</i></p> <p>3 <i>Spisula sachalinensis</i></p> <p>4 <i>Scaphechinus mirabilis</i></p> <p>5 <i>Nephtys caeca</i></p> <p>Diversity H' 1.74</p> <p>Polychaete type community</p> <p>1 <i>Ampharete arctica</i></p> <p>2 <i>Lumbrineris brevicira</i></p> <p>3 Gammarids</p> <p>4 <i>Nephtys caeca</i></p> <p>5 <i>Scaphechinus mirabilis</i></p> <p>Diversity H' 2.98</p>

Areal distributions of benthic communities sampled by means of Tamura grab in these four surf clam habitats and in the neighboring areas are shown in Fig. 44. The important species and diversity indices of surf clam habitat communities and the neighboring area are tabulated in Table 18.

Three community types are found in the surf clam beds in Ishikari Bay and on the coast of Tomakomai, two on the coast of Hachinohe and one in Hakodate Bay, respectively. The important species consisting in the same type communities in four surf clam beds are composed of the same species or very closely related species except *Tellina venulosa* of Pelecypod type community in Ishikari Bay and *Tecticeps japonica* of Gammarid type community on the coast of Tomakomai. On the other hand, communities in the area adjacent to the surf clam bed are distinctly different from surf clam bed communities in each region, and occasionally their principal species are not identical in the four regions. The surf clam bed communities indicate commonly lower species diversities and communities in the areas adjacent to surf clam beds distinctly show higher indices (Table 18). On the coast along Hachinohe, two communities which are structurally similar to those of three other surf clam beds are recognized in 1966, and Polychaete type community is observed in the area adjacent to surf clam bed (Fig. 44 and Table 18).

Whereas, in 1970 qualitative sampling of surf clam and macrobenthos was again carried out on the coast of Hachinohe in the same area as sampled in 1966. When compared the distribution of the surf clam population densities in 1966 (Fig. 43) with that in 1970 (Fig. 45), it can be easily understood that surf clam population shows a remarkable tendency to decrease, especially showing a sudden decrease less than 10 ind. per 100 m² in the area where surf clam formerly inhabited with dense population.

Comparatively high densities ranging from 20 to 10 individuals per 100 square meters are restricted to the narrow areas on the coast side (Fig. 45). While as is evident from Fig. 45, four benthic communities are distributed in 1970. Of these communities, Gammarid type, Pelecypod type and Polychaete type communities

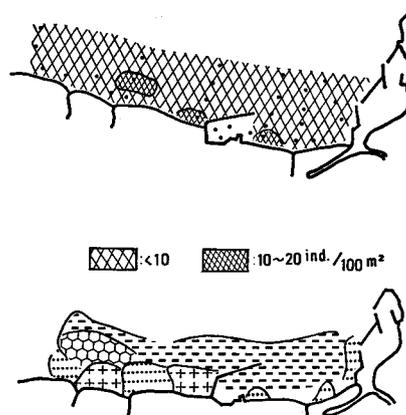


Fig. 45. Geographic distributions of number of individuals of surf clam (upper) and of benthic communities (under) in the coastal water of Hachinohe in 1970. Symbols as in Fig. 44.

are found in 1966, and *Scaphechinus* type community is observed in surf clam beds of Ishikari Bay and coastal region of Tomakomai. The areal extents of these communities are markedly different between 1966 and 1970. In other words, the areal extent of polychaete type community greatly expands coinciding with a decrease in the surf clam population. The areal extents of three other communities found in surf clam beds contract coinciding with a decrease in the surf clam population and are restricted to the narrow areas which show a somewhat high surf clam population.

In conclusion, in the scallop beds, freshwater clam beds and surf clam beds some similar communities in structure are observed respectively, even if the shellfish beds of the same pelecypod are geographically isolated from each other and the competent pelecypod is situated in the lower rank within the communities. This fact may indicate that the benthic communities found in the shellfish beds can be classified from the standpoint of their structural characters.

2. Discussion

In a certain shellfish ground, it is quite natural that the objective pelecypod species constitutes one of members of benthic community. It is, however, situated in the lower rank within the communities in shellfish bed except *Corbicula japonica* in the freshwater clam bed, which occupies the first rank within *Corbicula* type community. Whereas, the predominant members of benthic communities as observed in shellfish beds, which may have an influence on community type and species diversity, belong to the same genera or to very closely related species. Therefore the communities occurring in shellfish beds can be classified into a certain community basing on the community type and species diversity. Conversely, a good shellfish bed is recognized from the structural characteristics and the extent of occurrence of the benthic communities in time and space.

The above presumption may be supported by the contraction of communities in surf clam bed and the expansion of those outside of surf clam bed coincidentally with a decrease in surf clam population, as revealed on the coast of Hachinohe in 1966 and 1970. According to Odum (1971), the best way to control a particular organism, whether we wish to encourage or discourage it, is to modify the community, rather than to make a direct attack on the organism. Then, structural characteristics of the benthic communities in each shellfish bed may provide the effective informations for the control or the expansion of shellfish bed in order to encourage a particular pelecypod species occurring in the shellfish bed.

VII. Summary

For the accurate estimation of the organic material cycle in the benthic domain and for the application of benthic community to an indication of the environmental condition, structural characteristics of benthic communities first must be clarified in time and space, and then some real relationships between their characteristics and environmental elements must be examined.

From this viewpoint, structural characteristics of benthic communities were analyzed in temporal and spatial dynamic aspects and the correlations of their characteristics to environmental factors were determined.

The areas surveyed were Lagoon Zyusan-ko, Aomori Prefecture, and Hakodate Bay and Lake Notoro-ko, Hokkaido. In addition, the coastal regions of Hachinohe, Aomori Prefecture and Tomakomai, Hokkaido, and Ishikari Bay, Lake Saroma-ko and Lagoon Furen-ko, Hokkaido, where have a certain shellfish ground were surveyed.

The results obtained are summerized as follows

1. The bottom sediments in Zyusan-ko are mainly characterized by fine to coarse sand, poor organic matter and low total sulfide which are not seasonal in those areal distributions. Bottom water chlorinities fluctuate widely in time and space, whereas interstitial chlorinities are distinctly stable throughout the annual cycle, ranging from about 5‰ to 10‰ in the central part and nearly zero in the coastal region.

2. The particle compositions of the sediment in Notoro-ko are predominated by very fine sand in the regions with depth deeper than 10 m and by mediate to fine sand in the water shallower than 10 m, and not show significant differences between before and after of the construction of the mouth. Organic and total sulfide contents in the sediment show high in the central part and low in the coastal region, and not show seasonal and areal changes in their distributions. Their values, however, decrease distinctly in 1978 after the construction of the mouth. Chlorinities are roughly equal in value in time and space, and oxygen deficiency of bottom water found in summer 1972 disappears in 1978.

3. In Hakodate Bay, the particle compositions are predominated by fine to very fine sand in the central part and Hakodate Harbor, and predominated by coarse sand in the outer part and coastal region. Organic matter contents show high in the central part and Hakodate Harbor and decrease gradually toward the mouth and the shore. Chlorinities and oxygen contents in water vary slightly in time and space.

4. Benthos show a distinct difference in their areal distributions in every areas, for instance, in Zyusan-ko *Corbicula japonica* is mainly distributed in the eastern region, and Nemertinea A shows its central distribution in the central region, in Notoro-ko *Musculus senhousia* and *Pseudochironomus* sp. occur in large numbers in the shallow areas, while *Dorvillea japonica* and *Prionospio malmgreni* occur in the deep areas, and in Hakodate Bay four species of polychaetes show their central distributions in the central part and Hakodate Harbor, and two species of gammarids and *Mactra sinensis carneopicta* are mainly distributed in the shallow shore.

5. The structural characteristics of benthic communities in time and space are determined by means of community types and their species diversities, and consequently major communities in every areas are concluded as follows.

(1) Three community sereis are observed in Zyusan-ko. The first one consists of *Corbicula* type community with rather low diversity, which occurs on the shore and shows no seasonal changes in distribution. The second one occurs in the area from the shore to the central part showing comparatively high diversities. This consists of communities which are predominated by *H. similis* and *C. japonica* occurring during whole seasons, and *P. japonicus* occurring from fall to spring. The third one occurs in the central part showing comparatively high diversities. It is

seasonally predominated by *H. similis* and Nemertinea A all the year round, and *P. japonicus* from fall to spring.

(2) Two community series occur in Notoro-ko as observed in both 1972 and 1978. In 1972 one occurs on the shore. It consists of three communities which are mainly predominated by *M. senhousia* occurring from winter to summer and one community which is predominated by *Pseudochironomus* sp. occurring only in fall. The other occurs in the central part. It mainly consists of *Prionospio* type community predominated by *P. malmgreni* throughout the year. Diversities of two series show no difference in value. In 1978 one occurs widely in shallow region, consisting of similar communities which are commonly predominated by *M. tenuis*. The other mainly consists of community predominated by *D. japonica* and its extent coincides with that of azoic zone found in 1972.

(3) Three community series are observed in Hakodate Bay. Two series are not seasonal, and another one is seasonal in community composition. The first one consists of *Chaetozone* type community in somewhat low diversity and occurs in Hakodate Harbor, and the second one occurs on the shore consisting of communities predominated by one or two species of gammarids in low diversities. The third one in the central part consists of four communities of which structures are statistically similar to each other. *Chaetozone* sp. is the most principal member among them and the appearance of *M. sinensis carneopicta* is changed seasonally. This series shows comparatively high diversities.

6. In Zyusan-ko, interstitial chlorinities mainly influence the areal distribution of benthic communities and their species diversities.

In Notoro-ko, total sulfide content in the sediment is inferred limiting factor of the distribution of benthic communities and may strongly influence the species diversities.

Communities occurring in Hakodate Bay may be delimited by the particle composition and organic matter content in the sediment and a clear correlation between particulate diversity and species diversity is observed in this bay.

7. Benthic communities as observed in shellfish beds of scallop, surf clam and fresh water clam, consist of the predominant members which belong to the same genera or to very closely related species in each respective shellfish bed and their species diversities indicate roughly in value. Therefore, the communities occurring in shellfish beds of the same pelecypod, even if their beds are geographically isolated, can be classified into a certain community basing on the community type and species diversity.

8. The structural characteristics and the extent of occurrence of benthic communities in time and space are used to recognize a good shellfish bed. This presumption may be supported by the contraction of communities in surf clam bed and expansion of those outside surf clam bed coincidentally with the decrease of surf clam population, as revealed on the coast of Hachinohe in 1966 and 1970.

References

- Aoki, J. (1962). [Relation of community structure of moss mites to vegetation and soil in Oku-Nikko. II. Analyses of community structure of moss mites. (Horizontal comparison)]. *Jap. J. Ecol.*, **12**, 203-216. (in Japanese with German synopsis and summary).

- Asahina, E. (1941). An ecological study of *Corbicula japonica* group, the brackish water bivalve, with special reference to the environmental factors of its habitat in Hokkaido. *Bull. Japan Soc. Sci. Fish.*, **10**, 143-152. (in Japanese with English synopsis).
- Bader, R.G. (1954). The role of organic matter in determining the distribution of pelecypods in marine sediments. *J. Mar. Res.*, **13**, 32-47.
- Beadle, L.C. (1937). Adaptation to changes of salinity in the polychaetes I. Control of body volume and of body fluid concentration in *Nereis diversicolor*. *J. Exp. Biol.*, **14**, 56-70.
- Blegvad, H. (1928). Quantitative investigations of bottom invertebrates in the Limfjord 1910-1927 with special reference to plaice food. *Rep. Danish Biol. Stat.*, **31**, 27-56.
- . (1930). Quantitative investigations of bottom invertebrates in the Kattegat with special reference to the plaice food. *Rep. Danish Biol. Stat.*, **36**, 3-55.
- Bloom, S.A., Simon, J.L. & Hunter, V.D. (1972). Animal-sediment relations and community analysis of a Florida estuary. *Mar. Biol.*, **13**, 43-56.
- Boesch, D.F. (1977). A new look at the zonation of benthos along the estuarine gradient. In Coull, B.C. (ed.) *Ecology of marine benthos*, 245-266. Belle W. Baruch Library in Marine Science No. 6 Columbia, S.C.: University of South Carolina Press.
- Bowman, K.O., Hutcheson, K., Odum, E.P. & Shenton, L.R. (1970). Comments on the distribution of indices of diversity. In: *International Symposium on Statistical Ecology*, **3**, Pennsylvania State University Press.
- Crocker, R.A. (1967). Niche diversity in five sympatric of intertidal amphipods (Crustacea; Haustoriidae). *Ecol. Monogr.*, **37**, 173-200.
- Dales, R.P. (1962). The polychaete stomodeum and the interrelationships of the families of Polychaeta. *Proc. Zool. Soc. London*, **139**, 389-428.
- Davis, F.M. (1925). Quantitative studies on the fauna of the sea bottom. No. 2. Results of the investigations in the southern North Sea, 1921-24. *Fish. Invest. Lond.* Ser. 2, **8**, 50 p.
- Day, J.H., Field, J.G. & Montgomery, M.P. (1971). The use of numerical methods to determine the distribution of the benthic fauna across the continental shelf of North Carolina. *J. Animal Ecol.*, **40**, 93-125.
- Frankenberg, D. & Leiper, A.S. (1977). Seasonal cycles in benthic communities of the Georgia Continental Shelf. In Coull, B.C. (ed.), *Ecology of marine benthos*, 383-397. Belle W. Baruch Library in Marine Science No. 6 Columbia, S.C., University of South Carolina Press.
- Fuji, A. (1957). Changes in tissue chloride and physiological activity of the brackish-water bivalve, *Corbicula japonica*, in response to variations in salinity. *Bull. Fac. Fish. Hokkaido Univ.*, **8**, 163-177.
- Gray, J.S. (1974). Animal-sediment relationships. *Oceanogr. Mar. Biol. ann. Rev.*, **12**, 223-261.
- Gunter, G. (1945). Studies on marine fishes of Texas. *Publ. Inst. Mar. Sci. (Univ. Texas)*, **1**, 1-190.
- Habe, T. (1956). Studies on the shell remains in bays. *Res. Physiol. Ecol., Kyoto Univ.*, **77**, 1-31. (in Japanese with English res.)
- Hakodate Development Construction Office. (1979). [Business report of the tidal current in Hakodate Bay]. 80 p. (in Japanese).
- Hartman, O. (1955). Quantitative survey of the benthos of San Pedro Basin, Southern California. *Allan. Hanc. Paci. Exp.*, **19**, 1-185.
- Hayashi, I. (1978). Ecological distribution of macrobenthic animals on the level bottom in Turuga Bay. *Mem. Coll. Agri. Kyoto Univ.*, **112**, 1-27.
- Holland, A.F. & Polgar, T.T. (1976). Seasonal changes in structure of intertidal community. *Mar. Biol.*, **37**, 341-348.
- , Mountford, N.K. & Mikursky, J.A. (1977). Temporal variation in upper bay

- mesohaline benthic communities. I. The 9-m mud habitat. *Chesapeake Sci.*, **18**, 370-378.
- . & Dean, J.M. (1977). The community biology of intertidal macrofauna inhabiting sand bars in the North Inlet Area, South Carolina. In Coull, B.C. (ed), *Ecology of marine benthos*, 423-438, Belle W. Baruch Library in Marine Science No. 6, Columbia, S.C., University of South Carolina Press.
- Holme, N.A. (1953). The biomass of the bottom fauna in the English Channel off Plymouth. *J. mar. biol. Assoc. U.K.*, **32**, 1-49.
- Horikoshi, M. (1955). Marine communities in Moroiso-Aburatsubo Cove. *Bull. Biogeogr. Soc. Jap.*, **16-19**, 410-418.
- . (1962). Distribution of benthic organism and their remains at the entrance of Tokyo Bay, in relation to submarine topography, sediments and hydrography. *Nat. Sci. Rep. Ochanomizu Univ.*, **13**, 47-122.
- . (1970). Quantitative studies on the smaller macrobenthos inhabiting various topographical environments around the Sagami Bay. *J. Oceanogr. Soc. Jap.*, **26**, 159-182.
- Huling, N.C. & Gray, J.S. (ed.) (1971). A manual for the study of meiofauna. *Smithsonian Contrib. Zool.*, **78**, 1-83.
- Huston, M. (1979). A general hypothesis of species diversity. *American Naturalist*, **113**, 81-101.
- Hutcheson, K. (1970). A test for comparing diversities based on the Shannon formula. *J. Theor. Biol.*, **29**, 151-154.
- Ito, Y. (1976). [Animal ecology. Second volume]. 1st ed. 270 p. Kokin-Shoin. Tokyo. (in Japanese)
- Jacobowa, L. & Malm, E. (1931). Die Beziehungen einiger Benthosformen des Schwarzen Meeres zum Medium. *Bio. Zbl.*, **51**, 105-106.
- Jensen, B. (1919). Valuation of the Limfjord. 1. Studies on the fish-food in the Limfjord 1909-1917, its quantity, variation and animal production. *Rep. Danish Biol. Stat.*, **26**, 1-44.
- Johnson, R.G. (1970). Variation in diversity within benthic marine communities. *American Naturalist*, **104**, 185-300.
- . (1974). Particulate matter at the sediment-water interface in coastal environments. *J. mar. Res.*, **113**, 313-330.
- Kato, M., Matsuda, T. & Yamasita, Z. (1952). Associative ecology of insects found in the paddy field cultivated by various planting forms. *Sci. Rep. Tohoku Univ. Biol.*, **19**, 291-301.
- Kelley, D.W. (1966). Ecological studies of the Sacramento-San Joaquin estuary. Description of the Sacramento-San Joaquin estuary. *Fish. Bull. Calif. Dep. Fish Game*, **133**, 8-17.
- Kikuchi, T. (1964). Ecology and biological production of Lake Naka-umi and adjacent regions. 3. Macro-benthic communities of Lake Shinji-ko and Lake Naka-umi. *Spec. Publ. Seto. Mar. Biol. Lab.*, Ser. II, Part 1. 21-44.
- . (1969). Studies on the benthic animals community in the Hiuchi and Bingo Nada - 1968 -. (in Studies on the dynamics of the productivity of biotic community in inland sea area). *Rep. JIBP-PM*, 1968, 121-128.
- . (1976). [Benthic communities] In Motoda, S. (ed.) *Kaiso. Bentosu. Kaiyo-Kagaku-Kiso-Koza*, **5.**, 1st ed. 180-217. Tokai-daigaku-Shuppan-Kai. Tokyo. (in Japanese)
- . & Kikuchi, H. (1967). Bottom fauna of Lake Hinuma, Ibaraki Prefecture: The spring Aspect. *Jap. J. Ecol.*, **17**, 63-69. (in Japanese with English synopsis)
- . & Tanaka, M. (1978). Ecological studies on benthic macrofauna in Tomoe Cove, Amakusa I. Community structure and seasonal change of biomass. *Publ. Amakusa Mar. Biol. Lab.*, **4**, 189-213.

- Kinne, O. (1964). The effects of temperature and salinity on marine and brackish water animals. II. Salinity and temperature salinity combinations. *Oceanogr. Mar. Biol. Ann. Rev.*, **2**, 281-339.
- (1967). Physiology of estuarine organisms with special reference to salinity and temperature: general aspects. In *Estuaries* (Lauff, G.E. ed.), AAAS, Washington, 525-540.
- Kitamori, R. (1963). Studies on the benthos communities of littoral sea in the Seto Inland Sea and the adjacent waters. *Bull. Naikai Reg. Fish. Res. Lab.*, **21**, 1-90. (in Japanese).
- Kimoto, S. (1976). [Methods of study on animal community I. Diversity and species composition]. *Seitai-Gaku-Kenkyu-Ho-Koza* 14, 1st ed. 196 p. Kyoritsu-Shuppan. Tokyo. (in Japanese).
- Kosaka, M., Ogura, M., Daimon, K. & Miyasita, K. (1971). Studies on the benthic communities in Shimizu Harbour and Orido Bay I. Phase in summer. *J. Coll. Mar. Sci. Technol. Tokai Univ.*, **5**, 9-25. (in Japanese with English abstract)
- , ———, Arioka, H. & Fukuda, T. (1972). *Ditto*. II. Phase in winter. *Ibid.*, **6**, 51-61. (in Japanese with English abstract).
- Lloyd, M. & Chelardi, R.J. (1964). A table for calculating the equitability component of species diversity. *J. Anim. Ecol.*, **33**, 421-425.
- Margalef, D.R. (1958). Information theory in ecology. *Gen. Syst.*, **3**, 36-71.
- Mare, M.F. (1942). A study of a marine benthic community with special reference to the micro-organisms. *J. mar. biol. Ass. U.K.*, **25**, 517-554.
- McIntyre, A.D. (1969). Ecology of marine meiobenthos. *Biol. Rev.*, **44**, 245-290.
- McIntire, C.D. & Wulff, B.L. (1969). A laboratory method for the study of marine benthic diatoms. *Limnol. Oceanogr.*, **14**, 667-678.
- Mistakidis, M.N. (1951). Quantitative studies of the bottom fauna of Essex oyster grounds. *Gr. Britain Fish. Invest.*, **2**, 1-47.
- Miyadi, D. (1938). Quantitative studies on the benthic communities of the Osaka-wan I. *Umi to Sora*, **18**, 172-184. (in Japanese).
- (1940a). *Ditto*. II. *Nippon Gakuzyutu-Kyokai Hokoku*, **15**, 332-334. (in Japanese).
- (1940b). Marine benthic communities of the Osaka-wan. *J. Oceanogr.*, **12**, 1-15.
- (1940c). Soft bottom communities of the Tanabe-wan. *Shokubutsu to Dobutsu*, **8**, 33-39. (in Japanese)
- , Habe, T. and Yamaji, I. (1950). [Disharmonic bay and lagoon, and their improvement for fisheries purposes. On Kumigahama Bay]. In Okada, Y. (ed.) *Suisan-Dobutsu no Kenkyu*, 25-32. (Japanese)
- , Masui, T. & Habe, T. (1944). Embayment degree and community types in the bays. *Contrib. Physiol. Eco. Kyoto Imp. Univ.*, **3**, 1-19. (in Japanese).
- Möbius, K. (1877). Die Auster und die Austernwirtschaft. 126 pp., Hempel & Parrey, Berlin. (The oyster and oyster-culture. U.S. Commission Fish and Fisheries, pt. 8, Rept. of Commissioner 1880, 683-747).
- Molander, A.R. (1930). Animal communities on soft bottom areas in the Gullmar Fjord. *Kristinebergs Zoologiska Sta.*, 1877-1927, **2**, 1-90.
- Morisita, M. (1959). Measuring of interspecific association and similarity between communities. *Mem. Fac. Sci. Kyushu Univ., Ser. E*, **3**, 65-80.
- (1961). [Animal population]. In Miyadi, D. et al. (ed.) [*Animal ecology*]. 163-262. Asakura-Shoten. Tokyo. (in Japanese)
- Motomura, I. (1935). [Use of correlation coefficient in the statistics of animal community]. *Seitai-Gaku-Kenkyu*, **1**, 339-342. (in Japanese).
- Mountford, M.D. (1962). An index of similarity and its application to classificatory problems. In Murphy, P.W. (ed.) *Progress in Soil Zoology*. 43-50.
- Nakao, S. (1969). Benthic fauna of Sakhalin surf clam bed along the coast of Hachinohe, Aomori Prefecture. *Bull. Fac. Fish. Hokkaido Univ.*, **19**, 250-260. (in Japanese with English abstract)

- . (1976). Benthic communities in Hakodate Bay. *Physiol. Ecol. Japan*, **17**, 173-177. (in Japanese with English synopsis)
- . (1977). Polychaete species diversity and physical environment of sediment in Usu Bay. *Bull. Fac. Fish. Hokkaido Univ.*, **28**, 20-28. (in Japanese with English abstract)
- . (1979). Seasonal and spatial changes in the structure of mixohaline benthic communities. *Bull. Fac. Fish. Hokkaido Univ.*, **30**, 1-13.
- Odum, E.P. (1961). The role of tidal marshes in estuarine production. *The Conservationist*, **15**, 12-15.
- . (1971). *Fundamental of ecology*. 3rd ed. 588p. Toppan company. Tokyo.
- Okuda, S. (1935). Some lacustrine polychaetes with a list of brackishwater polychaetes found in Japan. *Ann. Zool. Jap.*, **14**, 240-246.
- Olive, P.J.W. (1971). Ovary structure and oogenesis in *Cirratulus cirratus* (Polychaeta: Cirratulidae). *Mar. Biol.*, **8**, 243-259.
- Petersen, C.G. Joh. (1913). Valuation of the sea, II. The animal communities of the sea bottom and their importance for marine zoogeography. *Rep. Danish Biol. Stat.*, **21**, 1-44.
- . (1918). The sea bottom and its production of fish-food. A survey of the work done in connection with the valuation of the Danish waters from 1883-1917. *Ibid.*, **25**, 1-62.
- Pielou, E.C. (1966). The measurement of diversity in different types of biological collections. *J. theor. Biol.*, **13**, 131-144.
- Reish, D.J. (1959). A discussion of the importance of the screen size in washing quantitative marine bottom samples. *Ecology*, **40**, 307-309.
- Remane, A. & Schlieper, C. (1971). *Biology of brackish water*. John Wiley and Sons. (Translation of Die Binnengewasser).
- Rosenberg, R. (1973). Succession in benthic macrofauna in a Swedish fjord subsequent to the closure of a sulphite pulp mill. *Oikos*, **24**, 244-258.
- Sanders, H.L. (1958). Benthic studies in Buzzards Bay, I. Animal-Sediment relationships. *Limnol. Oceanogr.*, **3**, 245-258.
- . (1960). *Ditto*. III. Structure of the soft-bottom community. *Ibid.*, **4**, 138-153.
- . (1968). Marine benthic diversity, A comparative study. *American Naturalist*, **102**, 243-282.
- Santos, S.L. & Simon, J.L. (1974). Distribution and abundance of the polychaetous annelids in a South Florida estuary. *Bull. Mar. Sci.*, **24**, 669-689.
- Sato, T. (1959). On the bottom sediments off the coast of Nosiro II. Especially on the classification of sandy sediments. *Hydro. Bull.*, **60**, 45-51. (in Japanese with English abstract).
- Seisi, R. and Tomiyama, T. (1942). On the unusual death of the oyster in relation to the sulfide contents in the bottom deposits of the brackish water Lake Hamanako, Sizuoka Prefecture. *J. Oceanogr. Soc. Jap.*, **1**, 75-84. (in Japanese)
- Shibuya, K. (1974). [Some problems of ecology]. New ed. 254 p. Rironsha. Tokyo. (in Japanese).
- Smith, R. (1955a). On the distribution of *Nereis diversicolor* in relation to salinity in the vicinity of Tvarmine, Finland, and the Isefjord, Denmark. *Biol. Bull.*, **108**, 326-345.
- . (1955b). Comparison of the level of chloride regulation by *Nereis diversicolor* in different parts of its geographical range. *Biol. Bull., Woods Hole*, **109**, 453-474.
- Tamura, T. (1953). On a new bottom snapper. *Bull. Fac. Fish. Hokkaido Univ.*, **3**, 240-242. (in Japanese)
- Tanita, S. & Okuda, T. (1956). Fundamental investigation on the marine resources of Matsushima Bay IV. Seasonal successions of water properties, bottom materials,

- and benthos. *Bull. Tohoku Reg. Fish. Res. Lab.*, **6**, 106-134. (in Japanese with English abstract).
- Tenore, K.R. (1972). Macrobenhtos of the Pamlico River estuary, North Carolina. *Ecol. Monogr.*, **42**, 51-69.
- Theede, H., Ponat, A., Hiroki, K. & Schlieper, C. (1969). Studies on the resistance of marine bottom invertebrates to oxygen-deficiency and hydrogen sulphide. *Mar. Biol.*, **2**, 325-337.
- Thorson, G. (1955a). Modern aspects of marine level-bottom animal communities. *J. Mar. Res.*, **14**, 387-397.
- . (1955b). Parallel level-bottom communities, their "balance" between predators and food animals. In Buzatti Traverso A.A. (ed.), *Perspectives in Marine Biology*, 621p., Univ. Calif. Press., Berkeley, 67-86.
- . (1957). Bottom communities (sublittoral or shallow shelf). *Geol. Soc. Amer. Mem.*, **67** (Treat. Mar. Ecol. Palaeoecol., vol. 1. Ecology, ed. by Hedgpeth, J.W.), 461-534.
- Ward, A.R. (1973). Studies on the sublittoral free-living nematodes of Liverpool Bay. 1. The structure and distribution of the nematode population. *Mar. Biol.*, **22**, 53-66.
- . (1975). *Ditto*. II. Influence of sediment composition on the distribution of marine nematodes. *Ibid.* **30**, 217-225.
- Welis, H.W. (1961). The fauna of oyster beds, with special reference to the salinity factor. *Ecol. Monogr.*, **31**, 239-266.
- Whitlatch, R.B. (1981). Animal-sediment relationships in intertidal marine benthic habitats: Some determinants of deposit-feeding species diversity. *J. exp. mar. Biol. Ecol.*, **53**, 31-45.
- Wieser, W. (1960). Benthic studies in Buzzards Bay. II. The meiofauna. *Limnol. Oceanogr.*, **5**, 121-137.
- Wigley, R.L. & McIntyre, A.D. (1964). Some quantitative comparisons of offshore meiobenthos and macrobenthos south of Martha's Vineyard. *Ibid.*, **9**, 485-493.
- Wilhm, J.L. (1967). Comparison of some diversity indices applied to populations of benthic macroinvertebrates in a stream receiving organic wastes, *J. Water Poll. Cont. Fed.*, **39**, 1673-1683.
- Winter, J.E. (1978). A review on the knowledge of suspension-feeding in lamellibranchiate bivalves, with special reference in artificial aquaculture systems. *Aquaculture*, **13**, 1-33.
- Yamamoto, G. (1950). Benthic communities in Mutsu Bay. *Sci. Rep. Tohoku Univ.*, (4th Ser. Biol.), **18**, 482-487.
- . (1951). Benthic communities in Mutsu Bay. *Bull. Japan Soc. Sci. Fish.*, **16**, 435-439.
- . (1952). Seasonal changes of benthonic communities and the succession in the benthos caused by the production of the Scallop. *Sci. Rep. Tohoku Univ.*, (4th Ser. Biol.), **19**, 302-314.
- . (1954). Ecological study of bottom communities in brackish water lakes III. Bottom communities of Obuchi-Numa and Takahoko-Numa, with special reference to the series of communities. *Jap. J. Ecol.*, **4**, 60-63. (in Japanese with English synopsis).
- . (1955). Fundamental investigation on he marine resources of Matsushima Bay II. Benthic communities in Matsushima Bay. *Bull. Tohoku Reg. Fish. Res. Lab.*, **5**, 208-214. (in Japanese with English rés.)
- . (1959). Behavior and mucus secretion of Japanese marsh clam, *Corbicula japonica* Prime. *Bull. Mar. Biol. Stat. Asamushi Tohoku Univ.*, **9**, 141-144.
- Yoshimura, S. & Wada, T. (1938). A contribution to the knowledges of the hidrogen sulphide and ferrous containd in the lacustrine deposits with special reference

- to those of brackish-water lakes. *Jap. J. Limnol.*, 8, 68-78. (in Japanese).
- Young, D.K. & Young, M.W. (1977). Community structure of the macrobenthos associated with seagrass of the Indian River Estuary, Florida. In Coull, B.C. (ed.), *Ecology of Marine Benthos*, 359-381. Belle W. Baruch Library in Marine Science No. 6 Columbia, S.C., University of South Carolina Press.