PHYTOSOCIOLOGICAL STUDY OF INTERTIDAL MARINE ALGAE
I. USUJIRI BENTEN-JIMA, HOKKAIDO

Yuzuru SAITO* and Susumu ATOBE*

Contents

I. Introduction

Intertidal marine, benthic algal, phytosociological studies in Japan have long been done (Taniguti, 1961; etc.) chiefly on algal zonation and its main regulating factor, "tide levels". This is an important problem that should be studied further. There are also other problems which should be studied with the above. To date there are only a few studies of standing crop, seasonal variation and succession (Kanda, 1947; Katada & Matsui, 1953 & 1954; Fukuhara, 1956; Uzike, 1956; Funano & Hasegawa, 1964; etc.) but there should be many more studies of these problems. Such work is especially rare along Tsugaru Strait where there are many interesting problems from the oceanographic point of view. We think the lack of an accepted or reliable method is one reason why such marine algal ecological studies are rare.

For several years, the senior author has tried to develop a convenient and reliable method for the study of intertidal algal communities. Finally, a modification of the belt transect method has been selected and applied to the study of the intertidal algal communities in Japan, especially in the area along Tsugaru Strait. The results can be used to characterize each rocky coast, its vegetation, productivity and its economical value as a place for algal culture.

The first survey using the technique selected was carried out at Usujiri Benten-Jima which is located near 140°57′E and 41°56′N in Southern Hokkaido (Fig. 1). The Faculty of Fisheries, Hokkaido University is planning to establish a new marine station there. The study also collected data for a summer training session for students which will take place in the near future. The main part of the study

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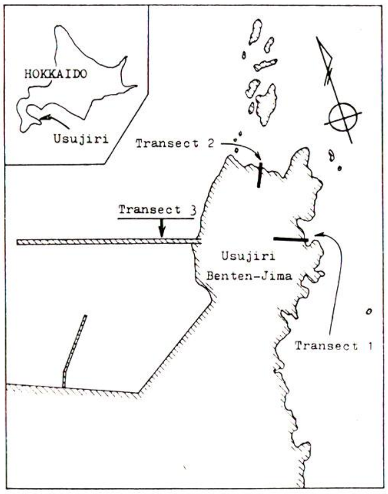

Fig. 1. A map showing the location and topography of Usujiri Benten-Jima with three transects. The length of the breakwater, on which the Transect 3 is located, is about 150 m.

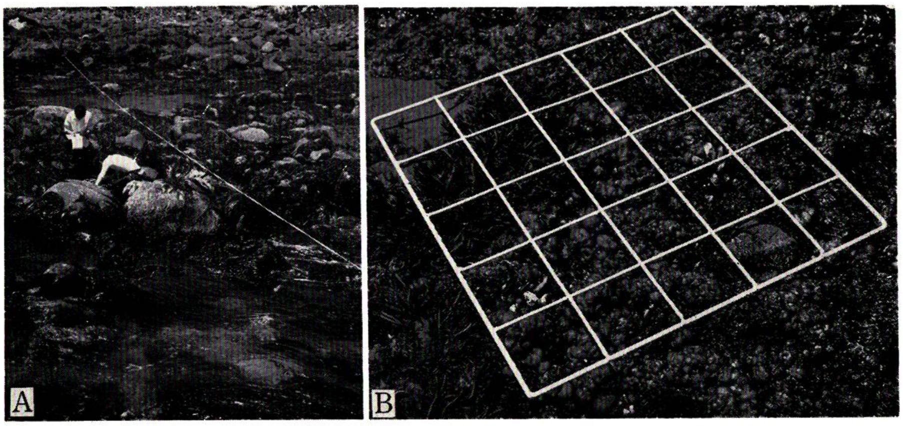

Fig. 2. **A.** Transect 1 shown by a tape measure stretched between two identifying points. **B.** The 50×50 cm iron quadrat used in the present study.

was done in July, 1968, along three transects in Benten-Jima. Seasonal variation of the algal communities was also observed from May, 1968 through May, 1969, along a transect in a relatively calm sea area.

We wish to express our sincere thanks to Dr. M. S. Doty of the University of Hawaii and Dr. I. A. Abbott of Hopkins Marine Station of Stanford University for reading and criticizing the manuscript. We are grateful to Mr. K. Taniguchi, one of our colleagues, for his constant assistance in the field work. Thanks are also due to Dr. J Tokida, Dr. T. Masaki, Dr. H. Yabu and Mr. H. Yamamoto of

Hokkaido University for their advice and encouragement.

II. Method

Vertically the intertidal marine algal communities have, as a rule, extremely condensed zonation. A line or belt transect method was considered particularly desirable for the study and description of such communities. For use we modified the belt transect method slightly, because the plant coverage of the whole study area can be seen easily while standing in one place. The transect to be studied was laid out at right angles to the zones. Before the observation process was begun, a tape measure was stretched between two easily recognizable points on prominent rocks; one higher than EHWS* and the other lower than ELWS**. Transects 1 and 2 were placed as shown in Fig. 1. A photograph of the former is shown in Fig. 2, A. A profile was drawn along each transect using land surveying methods. The first observation was made at the highest (or inland) limit of the algal communities. Subsequent observations were made along the transect at intervals of 2.0 meters (along Transect 1) or 1.5 meters (along Transect 2) from the first station. There were fifteen stations along Transect 1 and seventeen along Transect 2 (Figs. 4–7). The observations being at the intervals given saved considerable time. The main part of the study was done in the littoral zone as this is defined by T. & A. Stephenson (1949).

Observations were made using a square 50×50 cm iron quadrat divided into twenty-five 10×10 cm areas (Fig. 2, B). The quarat was placed at each station (Fig. 3, B) and the occurrence of each species was noted in each of the twenty-five

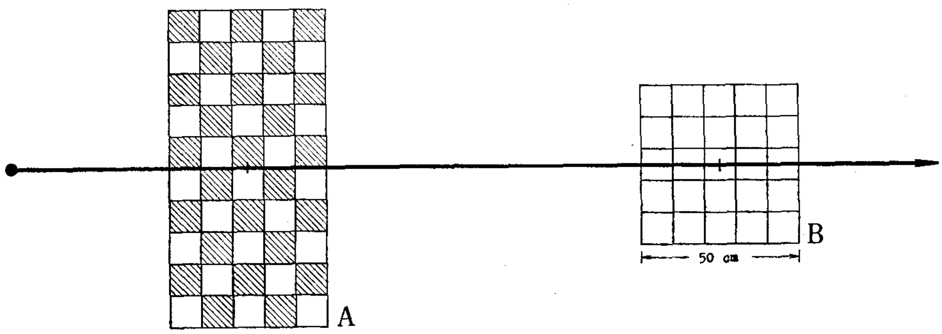

Fig. 3. Showing the location of a station using the tape measure. At most stations, the observations were made in the area shown by A; but sometimes, especially for a simple comunity, B was used.

* Extreme high water of spring tides at Usujiri was 147 cm above the datum plane for the tide table during the period of May, 1968, through April, 1969.

** Extreme low water of spring tides at Usujiri was 22 cm below the datum plane for the tide table during the period of May, 1968, through April, 1969.

small areas. While observations were regularly recorded from twenty-five small areas, we used two 50×50 cm quadrats at as many as possible.

In recording the algal coverage, the following numbers to indicate degree of dominance or cover were used:

5: Covering 1/2–1/1 of the substratum surface.
4: Covering 1/4–1/2 of the substratum surface.
3: Covering 1/8–1/4 of the substratum surface.
2: Covering 1/16–1/8 of the substratum surface.
1: Covering less than 1/16 of the substratum surface.

The above five classes of dominance may seem too rough or coarse. Finer classes or more classes might seem better especially in expressing quantity. However more classes would require much more time and skill, which was impractical because of the short ebb tide period. Moreover, the results might be more and inacceptably variable depending on the observer. Therefore, we used the above classes which provided results quickly and practically.

From the results, both the frequency (=F) and the coverage (=C) of each species in each 50×50 cm quadrat were calculated in the following way:

$$F = \frac{qn}{25} \times 100 = 4 \cdot qn$$

$$C = \frac{c_1}{25} + \frac{c_2}{25} + \cdots + \frac{c_{qn}}{25}$$

qn: number of 10×10 cm areas in which the corresponding species appeared. $c_1, c_2, \ldots c_{qn}$: median value of percentage of each class of dominance as follows:

5: 75% (c/25: 3)
4: 37.5% (c/25: 1.5)
3: 18.75% (c/25: 0.75)
2: 9.375% (c/25: 0.375)
1: 4.6875% (c/25: 0.1875)

We used the numbers 1, 2, 3, 4 and 5 as indices to show algal coverage in the field and then substituted the percentage for them after returning to the laboratory. There are problems in calculating the coverage. For example, any caespitose species growing abundantly in a quadrat will be represented by 75% coverage, and for a species with small thalli with one individual each, growing in all twenty-five of the 10×10 cm areas will be recorded as having 5% coverage. This is a result of counting fractions of 0.5 and over as 1.0 and disregarding those of less than 0.5. In the field, such conditions are very few and if when they do exist the ranking of the species is not changed very often. To avoid errors, the mark "+" was used for any coverage of less than 5%.

For example, both frequency and coverage of *Leathesia difformis* and *Gloiopeltis* *furcata* in Fig. 2, B are recorded and calculated as follows in respect to their occurrence in the quadrat:

Leathesia difformis

0	1	2	2	3	$F = 4\times22 = 88$
0	0	3	2	2	$C = 3\times6+1.5\times3+0.75\times3+0.375\times6+0.1875\times4$
1	2	5	4	5	$= 27.75 \fallingdotseq 28$
3	5	5	1	4	
5	5	4	1	2	

Gloiopletis furcata

3	5	3	4	2	$F = 4\times16 = 64$
5	5	2	4	4	$C = 3\times4+1.5\times3+0.75\times2+0.375\times4+0.1875\times3$
5	2	2	0	0	$= 20.0625 \fallingdotseq 20$
1	0	0	0	0	
1	1	0	0	0	

Transect 3 (Fig. 1) was on the outer side of a breakwater. On this vertical transect, we observed fifteen 10×10 cm areas for each 10 cm in vertical height in the algal communities from their highest limit downwards to 2 meters below the datum plane of the tide table. The results were arranged like those along Transects 1 and 2, however, the denominators of expression were changed into 15, instead of 25.

A separate study was made on July 10, 1968, at five stations near Transect 1, to clarify the relationship between the algal coverage and species presence. After recording algal community using the above quadrat method, the plants were gathered for measuring wet and dry weights.

Seasonal observations were made along Transect 1, as a rule once a month.

III. Results

1. Transect 1

a) The detailed study on July 10, 1968. The algal communities together with a physical profile are shown in Fig 4. This transect cuts across three tide pools at different heights. In the tide pool which lies between 13.5 and 17.5 meters from the starting point, the water temperature was more than 30°C at ebb tide in the daytime while in the open sea it was 18°C. Stations 1 and 2 are situated in this pool. The vegetation at both stations was simple; *Chaetomorpha moniligera* was abundant, 70% in frequency, but not abundant in coverage. Station 3 is situated in the second tide pool which lies between 22.2 and 24 meters from the starting point. Throughout this station, *Scytosiphon lomentaria* formed a pure and dense community. *Gloiopeltis furcata* dominated from Stations 4 to 6 and a pure community occupied Station 4. *Heterochordaria abietina* occurred at Station 5 and was found at most of the stations thence outward. The third tide pool lies

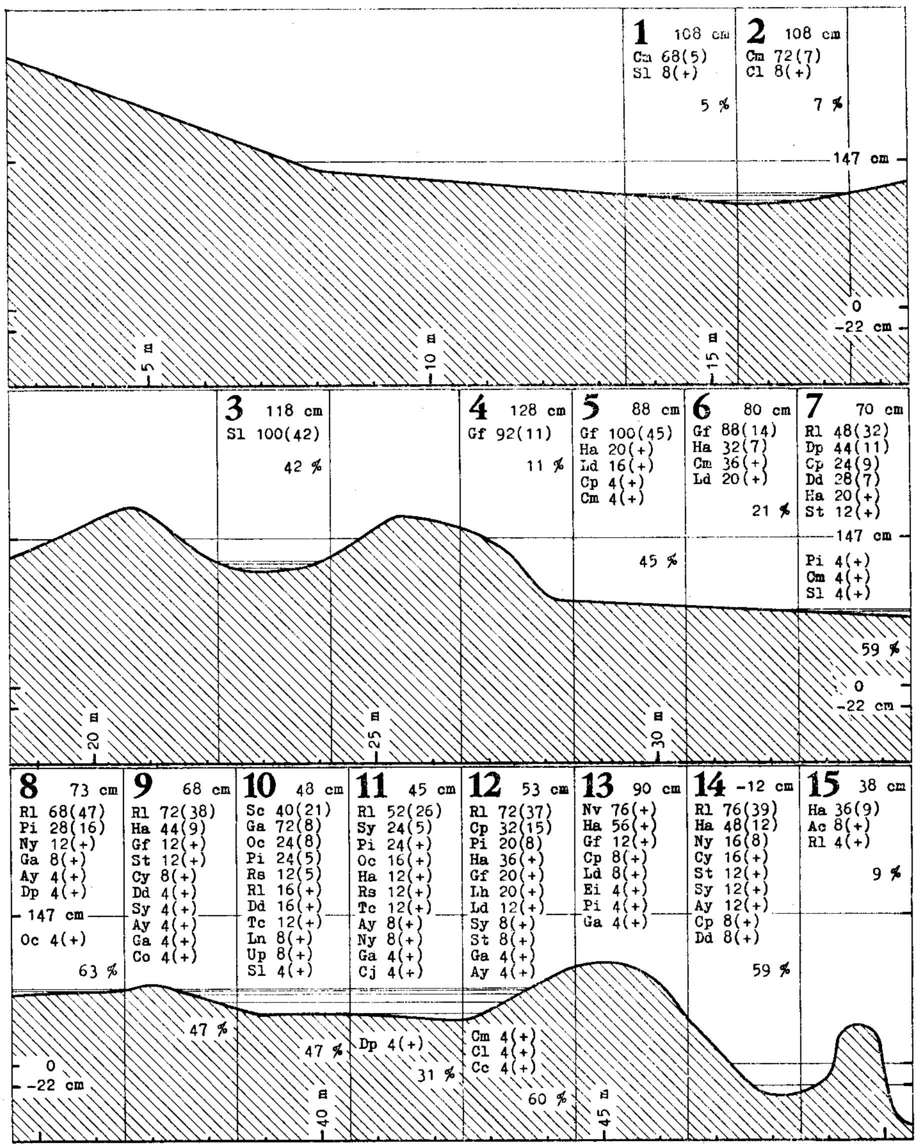

Fig. 4. Algal communities at 15 stations along Transect 1 for July 10, 1968, drawn over a profile of the substratum. The large numbers are station numbers and the height of each station from the datum level is shown on the right hand side, while the algal species are shown below each quadrat number with their frequency and coverage (in parenthesis). Both of the latter are in per cent. The total coverage in per cent for each station is found at the bottom. The measure shows the EHWS (147 cm), the datum sea level (0) and the ELWS (-22 cm), respectively. Ac: *Alaria crassifolia*. Ay: *Acrosorium yendoi*. Cc: *Chondrus crispus*. Cj: *Ceramium japonicum*. Cl: *Cladophora opaca*. Cm: *Chaetomorpha moniligera*. Co: *Chondrus ocellatus*. Cp: *Corallina pilulifera*. Cy: *Chondrus yendoi*. Dd: *Dictyota dichotoma*. Dp: *Dictyopteris divaricata*. Ei: *Enteromorpha intestinalis*.

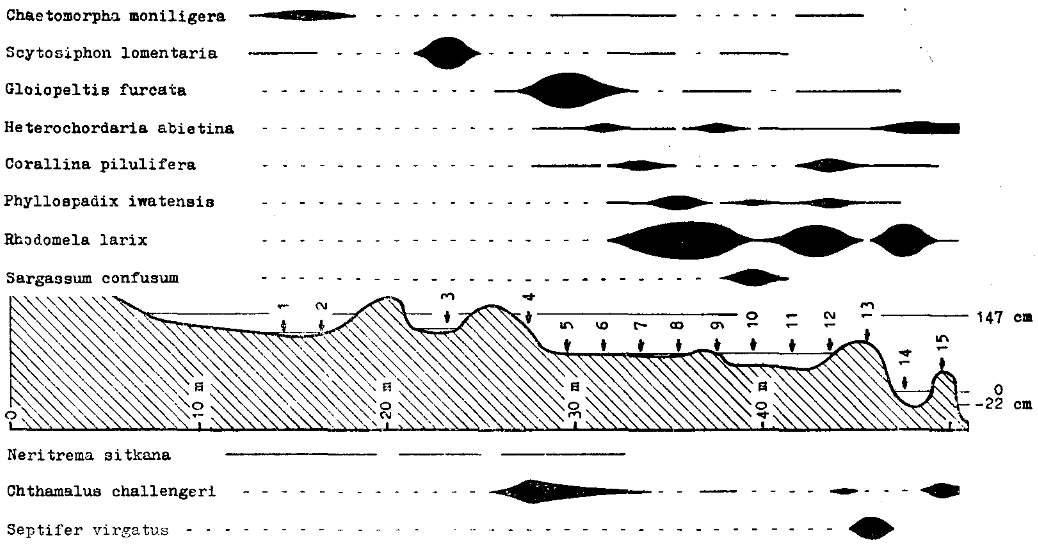

Fig. 5. A diagram showing the distribution pattern of major species along Transect 1, on July 10, 1968. Intertidal animals are shown below the substratum profile (determined by Messers T. Igarashi and T. Iwaki of the Faculty of Fisheries, Hokkaido University).

between 32 and 43 meters from the starting point. In the profile near 37 meters (Fig. 4), this pool is divided at Station 9 into two parts by an island. There are some differences between the landward and seaward sides of this island. The two stations on the landward side (7 and 8) bore *Dictyopteris divaricata*, while a few *Dictyota dichotoma* were growing at Stations 9 and 10 on the seaward side. Moreover, between Stations 9 and 12 some of the species seemed to be lower littoral or sublittoral species. For example, *Sargassum confusum* (dominant at Station 10), *Gelidium amansii* (also present at Station 8 on the landward side, but not abundant there), as well as *Odonthalia corymbifera*, *Rhodomela subfusca*, *Tichocarpus crinitus*, *Laurencia nipponica* and *Ceramium japonicum* which normally occur lower were found here. *Rhodomela larix* occurred at all stations on both sides of the island and was the dominant species at most stations in the pool. This species also occurred abundantly at Station 14 which was usually below the water surface even during an ebb tide period and Station 15 had a trace of it. Station 13 (on the rock bench) was poor in algal coverage and was characterized by the presence of *Nemalion vermiculare*. The projecting portion along this transect (Stations 9,

Fig. 4

Ga: *Gelidium amansii*. Gf: *Gloiopeltis furcata*. Ha: *Heterochordaria abietina*. Ld: *Leathesia difformis*. Lh: *Lomentaria hakodatensis*. Ln: *Laurencia nipponica*. Nv: *Nemalion vermiculare*. Ny: *Neodilsea yendoana*. Oc: *Odonthalia corymbifera*. Pi: *Phyllospadix iwatensis*. Rl: *Rhodomela larix*. Rs: *Rhodomela subfusca*. Sc: *Sargassum confusum*. Sl: *Scytosiphon lomentaria*. St: *Sargassum thunbergii*. Sy: *Symphyocladia latuiscula*. Tc: *Tichocarpus crinitus*. Up: *Ulva pertusa*.

Table 1. The frequency, coverage and standing crop of the algal communities on the N-E coast of Usujiri Benten-Jima, on July 10, 1968 (in 50×50 cm quadrat)

Station	Species	F	C	W.W.	D.W.	D.W./C
St. A	*Rhodomela larix*	72	49	745	155	3.2
	Heterochordaria abietina	44	22	240	56	2.5
	Chondrus yendoi	16	7	40	15	2.1
	Neodilsea yendoana	16	+	115	23	–
	Acrosorium yendoi	12	+	+	+	–
	Gymnogongrus flabelliformis	4	+	+	+	–
	Symphyocladia latiuscula	4	+	+	+	–
	Total	–	78	1140	249	3.2
St. B	*Phyllospadix iwatensis*	56	34	3720	970	28.5
	Neodilsea yendoana	24	11	105	22	2.0
	Laurencia nipponica	24	7	40	6	0.9
	Sargassum confusum	12	7	430	79	11.3
	Rhodomela larix	16	6	95	25	4.2
	Rhodomela subfusca	8	+	55	8	–
	Odonthalia corymbifera	8	+	40	10	–
	Total	–	65	4485	1120	17.2
St. C	*Rhodomela larix*	92	55	960	180	3.3
	Dictyopteris divaricata	44	14	135	23	1.6
	Sargassum thunbergii	20	5	170	30	6.0
	Heterochordaria abietina	16	+	6	1	–
	Chaetomorpha moniligera	4	+	+	+	–
	Phyllospadix iwatensis	4	+	+	+	–
	Total	–	74	1271	234	3.2
St. D	*Rhodomela larix*	52	30	512	102	3.4
	Dictyopteris divaricata	40	12	142	21	1.8
	Heterochordaria abietina	28	6	60	14	2.3
	Corallina pilulifera	24	6	33	13	2.2
	Sargassum confusum	12	+	+	+	+
	Total	–	54	747	150	2.8
St. E	*Gloiopeltis furcata*	100	53	317	115	2.2

St. A is close to St. 14 of Transect 1. St. B and St. C are in deeper portion of the largest tide pool in which St. 10 and St. 11 of Transect 1 are located. St. D is in a much shallower portion of the above tide pool, and is close to St. 7 of Transect 1. St. E is close to St. 5 of Transect 1. F: Frequency in percent. C: Coverage in percent. W.W.: Wet weight in g. D.W.: Dry weight in g. D.W./C: Coverage (%) and dry weight (g) ratio.

12 and 13) bore a few thalli of *Gloiopeltis furcata* which was the dominant species at Stations 4, 5 and 6. Algal coverage seemed to increase toward low tide mark and diminished at Station 13 and 15 which are on upward projections of the substratum.

The distribution of the major species is summarized in Fig. 5 using their coverages. That of the conspicuous benthic animals is also shown below the

Table 2. Seasonal variation of major species of intertidal plants along Transect 1, during the period between May 3, 1968 and May 4, 1969, shown in frequency (F) and coverage (C) percent.

Species \ Study Date		1968							1969		
		May 3rd	Jun. 14th	Jul. 10th	Aug. 13th	Sep. 22nd	Nov. 20th	Dec. 18th	Feb. 3rd	Apr. 6th	May 4th
Monostroma angicava	F	27	1	—	—	—	—	—	—	16	13
	C	3.9	+	—	—	—	—	—	—	0.4	0.8
Enteromorpha intestinalis	F	5	4	1	—	—	—	—	—	—	—
	C	+	0.5	+	—	—	—	—	—	—	—
Cladophora opaca	F	1	1	1	—	—	—	—	—	—	—
Chaetomorpha moniligera	F	—	7	12	18	8	—	—	—	—	—
	C	—	0.5	0.8	+	+	—	—	—	—	—
Dictyota dichotoma	F	—	—	4	8	14	14	10	8	—	—
	C	—	—	0.5	+	2.1	2.5	1.4	0.7	—	—
Dictyopteris divaricata	F	6	6	3	4	2	4	3	10	5	3
	C	1.7	1.3	0.7	1.2	+	+	+	1.9	1.2	0.5
Leathesia difformis	F	2	5	4	1	1	—	—	—	1	2
Heterochordaria abietina	F	25	20	20	21	21	17	13	19	19	20
	C	3.2	5.6	2.5	2.2	0.8	1.1	0.9	1.8	2.6	2.7
Scytosiphon lomentaria	F	18	16	8	2	1	—	2	7	7	9
	C	6.8	6.1	2.8	+	+	—	+	0.5	1.7	2.3
Colpomenia bullosa	F	5	—	—	—	—	1	1	2	5	1
	C	0.8	—	—	—	—	+	+	+	+	+
Sargassum confusum	F	3	4	3	3	3	2	3	1	3	2
	C	+	0.7	0.8	0.3	0.3	+	+	+	+	+
Sargassum thunbergii	F	2	3	3	2	2	2	1	—	—	1
Bangia fusco-purpurea	F	8	2	—	—	—	—	—	—	9	9
	C	0.9	+	—	—	—	—	—	—	2.0	2.3
Porphyra yezoensis	F	2	6	—	—	—	—	1	1	2	5
Nemalion vermiculare	F	—	—	5	6	5	—	—	—	—	—
	C	—	—	+	0.4	+	—	—	—	—	—
Gelidium amansii	F	6	9	6	3	8	4	2	3	5	5
	C	0.7	2.1	0.5	+	0.5	+	+	+	0.5	0.5
Dumontia simplex	F	4	2	—	—	—	1	5	6	7	7
	C	0.6	+	—	—	—	+	+	+	0.7	0.5
Neodilsea yendoana	F	3	2	2	2	4	3	1	1	4	4
	C	+	+	+	+	+	+	+	+	0.3	+
Corallina pilulifera	F	6	8	5	21	27	21	23	25	18	21
	C	+	1.6	1.6	1.7	1.7	1.9	2.0	1.6	0.7	1.9
Gloiopeltis furcata	F	23	22	19	23	22	23	24	28	22	19
	C	4.6	7.6	4.7	3.4	2.3	3.6	4.2	7.3	6.5	4.8
Tichocarpus crinitus	F	1	1	2	—	2	4	2	3	2	2
Chondrus yendoi	F	2	1	2	1	1	1	2	3	1	1
Lomentaria hakodatensis	F	—	—	1	1	2	2	2	—	—	—

Table. 2 (Continued)

Acrosorium yendoi	F	1	3	4	1	3	3	4	3	1	1
Chondria crassicaulis	F	2	1	1	1	2	4	2	5	3	1
Laurencia nipponica	F	1	1	1	1	–	–	–	1	1	1
Symphylocaldia latiuscula ..	F	4	4	3	2	4	5	3	1	5	3
	C	+	+	0.3	+	+	+	+	+	+	+
Rhodomela larix	F	25	21	27	23	25	24	24	16	24	22
	C	**7.4**	**11.4**	**14.6**	**10.5**	**7.1**	**4.9**	**3.5**	**2.3**	**5.1**	**5.8**
Rhodomela subfusca	F	8	10	2	2	3	5	4	6	4	4
	C	1.3	2.5	0.3	0.3	+	+	+	+	+	+
Odonthalia corymbifera	F	1	5	3	4	2	2	3	4	3	3
	C	+	0.3	0.5	0.3	+	+	+	+	+	+
Phyllospadix iwatensis ..	F	9	9	7	8	4	7	4	6	3	5
	C	*2.9*	*3.1*	1.6	**3.6**	0.5	+	+	0.4	0.4	0.3
Total coverage		34.8	43.3	32.7	23.9	15.3	14.0	12.0	16.5	22.1	22.4

The coverage of species represented only by frequency (F) is equal to "+". A coverage in boldface shows which species are dominant and the specific names in boldface are those of dominant species found at least once during the study period. The italicized coverage is that of subdominant species.

physical profile on this figure. Coverage was not detailed for them. The habitat elevations of the benthic animals are as follows:

Neritrema sitkana (Philippi): 80–190 cm above the datum level
Chthamalus challengeri Hoek: 80–140 cm 〃 〃
Septifer virgatus (Wiegmann): 100–110 cm 〃 〃

The lower limit of the terrestrial lichens, e.g., *Parmelia*, is 200 cm above the datum level. Some flowering plants of the genus *Artemisia*, *Atriplex* as well as other genera are found 230 cm above the datum level, thus even their lowest levels could not be included in the figures.

Measurements of the standing crop near Transect 1 are shown in Table 1, in respect to wet and dry weights per 1/4 square meter.

b) Seasonal observations of the algal communities. Seasonal variation was recorded monthly from May 3, 1968, through May 4, 1969. In October, 1968, January and March, 1969, we could not make the observations because of stormy weather. Although the frequency and the coverage by each alga as well as total coverage showed a seasonal variation, there was no essential variation in the distributional pattern along the transect. So, the results obtained are summarized in Table 2, in terms of frequency and coverage averaged for the whole transect.

2. Transect 2

The algal communities along Transect 2 were observed on July 11, 1968.

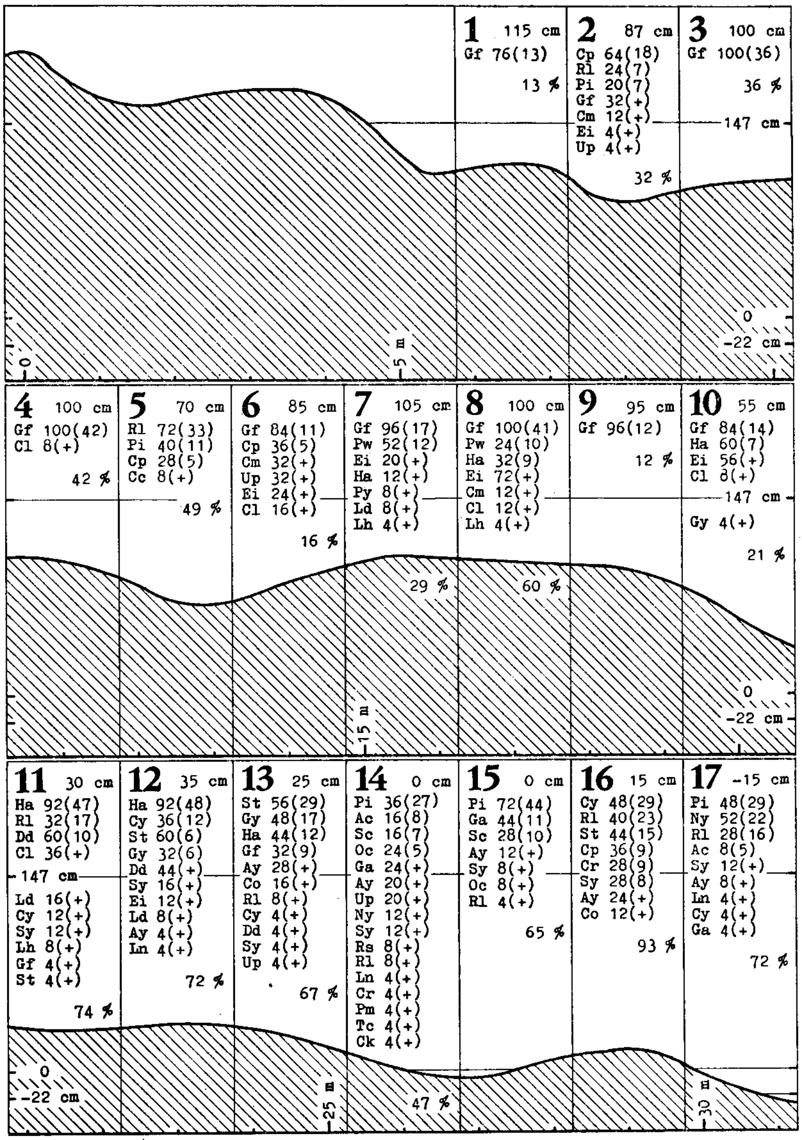

Fig. 6. Algal communities at 17 stations along Transect 2 for July 11, 1968, drawn over a profile of the substratum. Ck: *Ceramium kondoi*. Cr: *Chondrus pinnulatus* f. *armatus*. Gy: *Gymnogongrus flabelliformis*. Pm: *Polysiphonia morrowii*. Pw: *Pelvetia wrightii*. Py: *Porphyra yezoensis*. See the explanation in Fig. 4, for further abbreviations and explanation of other expressions.

The results obtained, together with the profile are shown in Fig. 6. There is no conspicuous tide pool along this transect. In the higher area (between Stations 1 and 10), *Gloiopeltis furcata* was dominant both in frequency and coverage, except

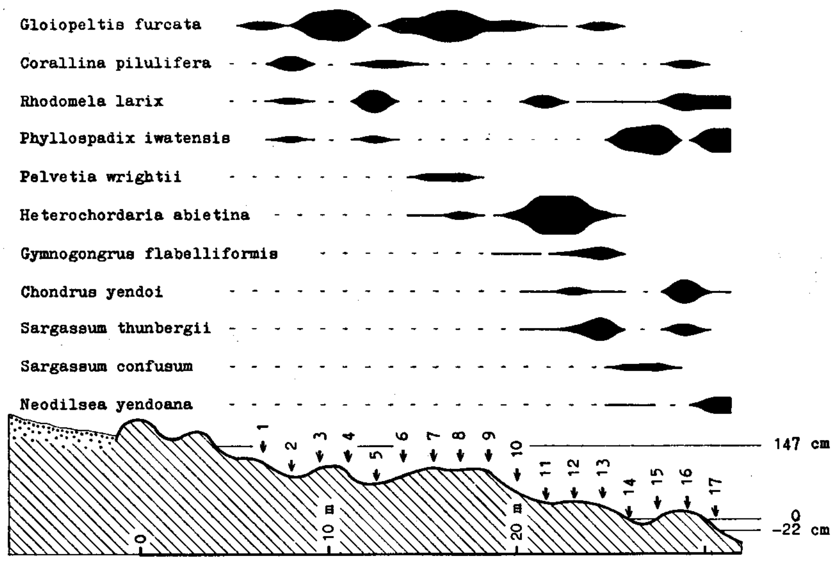

Fig. 7. A diagram showing the distribution pattern of major species along Transect 2, on July 11, 1968.

at Stations 2 and 5. The stations in the depression (2, 5 and 6) have some thalli of *Corallina pilulifera*, which was dominant at Station 2. Two stations (2 and 5) have *Rhodomela larix*, which was dominant at Station 5. Although *Phyllospadix iwatensis* was found at Stations 2 and 5, it was smaller in size than when found still lower. A pure community of *Gloiopeltis furcata* was present at Stations 1, 3 and 9. Station 9 has many barnacles (*Chthamalus challengeri*). *Pelvetia wrightii* grew at Stations 7 and 8, along with *Gloiopeltis furcata*. *Heterochordaria abietina* appeared at Station 7 and became abundant in lower areas, where it was most abundant at Stations 11 and 12. It occurred as far down as Station 13, which was also the lowermost limit of *Gloiopeltis furcata*. *Sargassum thunbergii* was dominant both at Stations 13 and 16. *Phyllospadix iwatensis* was dominant at Stations 14, 15 and 17. Stations 14 and 15 had *Sargassum confusum*. *Chondrus yendoi* was dominant at Station 16 and was also distributed at Stations 11, 12, 13 and 17. Total coverage seemed to increase toward lower areas.

The distributions of the major species are summarized in Fig. 7 by their coverages.

3. Transect 3

The algal communities along Transect 3 were observed on the 11th and 12th of July, 1968. The results obtained are shown in Fig. 8. Along this vertical transect, a few thalli of *Nemalion vermiculare, Leathesia difformis* and *Ulva pertusa* appeared in the highest zone (between 100 and 110 cm). *Leathesia difformis* disappeared below the 30 cm level, after a slight increase in the zone between 60

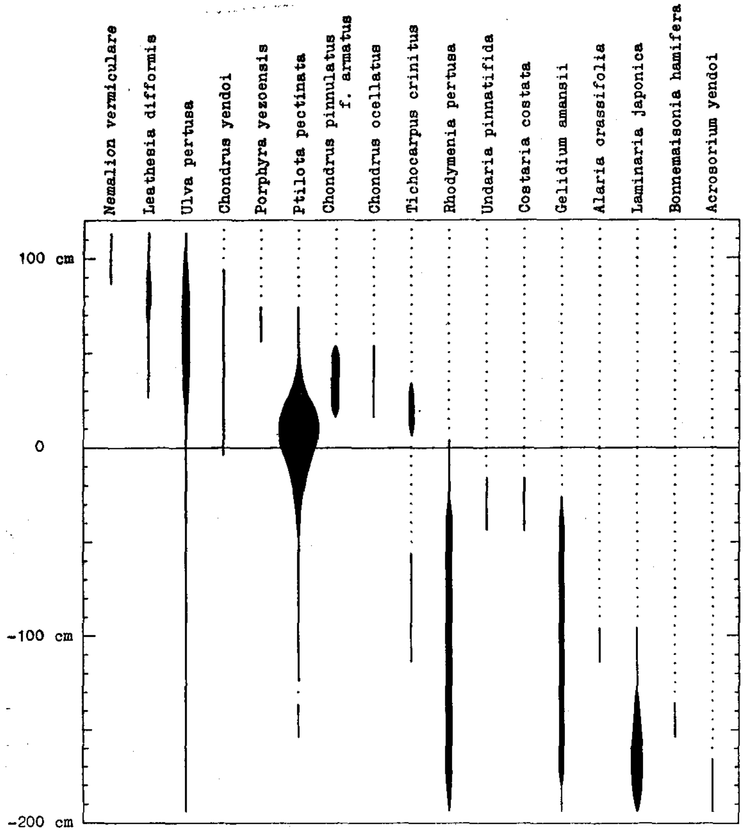

Fig. 8. A diagram showing vertical distribution of the algae along Transect 3, on July 11 and 12, 1968.

and 70 cm. *Ulva pertusa* had about 7–9% coverage between 30 and 90 cm, diminished below this but occurred as low as -190 cm. *Chondrus yendoi* appeared between 0 and 90 cm, but was not abundant. A single individual of *Porphyra yezoensis* was observed between 60 and 70 cm. *Ptilota pectinata*, the most dominant species along this transect, occurred between 60 and 70 cm, increased below this and covered approximately 50% of the zone between 0 and 20 cm. It was observed as low as -150 cm but gradually diminished below the ELWS level. *Chondrus pinnulatus* f. *armatus* and *Chondrus ocellatus* occurred between 20 and 50 cm. *Tichocarpus crinitus* appeared twice along this transect, once between 10 and 20 cm and once between -100 and -50 cm. The abundant species below the datum level were *Rhodymenia pertusa* and *Gelidium amansii*. Although the former appeared in higher place than the latter, both species increased along with the decrease of *Ptilota pectinata* downward from the ELWS. Among the Laminariales, a few (*Undaria pinnatifida* and *Costaria costata*) occurred between -40 and

Table 3. Frequency and coverage (in parenthesis) of the algal community above the ELWS of Transect 3.

Height in cm	Nv	Ld	Up	Cy	Py	Pp	Cr	Co	Tc	Rp
110–100	7(+)	27(+)	33(+)							
100–90	7(+)	60(+)	67(5)							
90–80		93(5)	100(8)	20(+)						
80–70		100(5)	100(9)	47(+)						
70–60		73(+)	100(8)	47(+)	7(+)	27(+)				
60–50		53(+)	100(8)	27(+)		60(+)				
50–40		20(+)	100(8)	20(+)		93(6)	20(8)	27(+)		
40–30		13(+)	73(7)	20(+)		100(9)	27(8)	27(+)		
30–20			40(5)	27(+)		100(27)	20(8)	27(+)	27(5)	
20–10			13(+)	7(+)		100(47)			27(5)	
10–0			13(+)	7(+)		100(47)				
0–-10			13(+)			100(38)				7(+)
-10–-20			7(+)			93(18)				7(+)

Pp: *Ptilota pectinata.* Rp: *Rhodymenia pertusa.* See the explanations in Fig. 4 and Fig. 6, for further abbreviations.

-20 cm. *Alaria crassifolia* and *Laminaria japonica* were found between -110 and -100 cm, and the latter increased downward. One individual of *Bonnemaisonia hamifera* was observed between -150 and -140 cm. A few thalli of *Acrosorium yendoi* were present below -170 cm. Below -190 cm, no algae were observed.

Among the algal communities along Transect 3, those above the ELWS level are shown in detail in Table 3.

IV. Discussion

1. Vertical distribution

a) Comparison of the vertical distributions along the three transests.

A diagram of the vertical distribution of the major species along both Transects 1 and 2 is shown in Fig. 9. The species are arranged according to the elevation of the centers of each 50×50 cm station in which the corresponding species occurred.

In this diagram, it is clear that most species which appear more than 90 cm above the datum level, usually occur at higher places on Transect 2 than on Transect 1. There are some exceptions such as *Gloiopeltis furcata, Chaetomorpha moniligera* and *Cladophora opaca.* The latter two occur between 100 and 110 cm

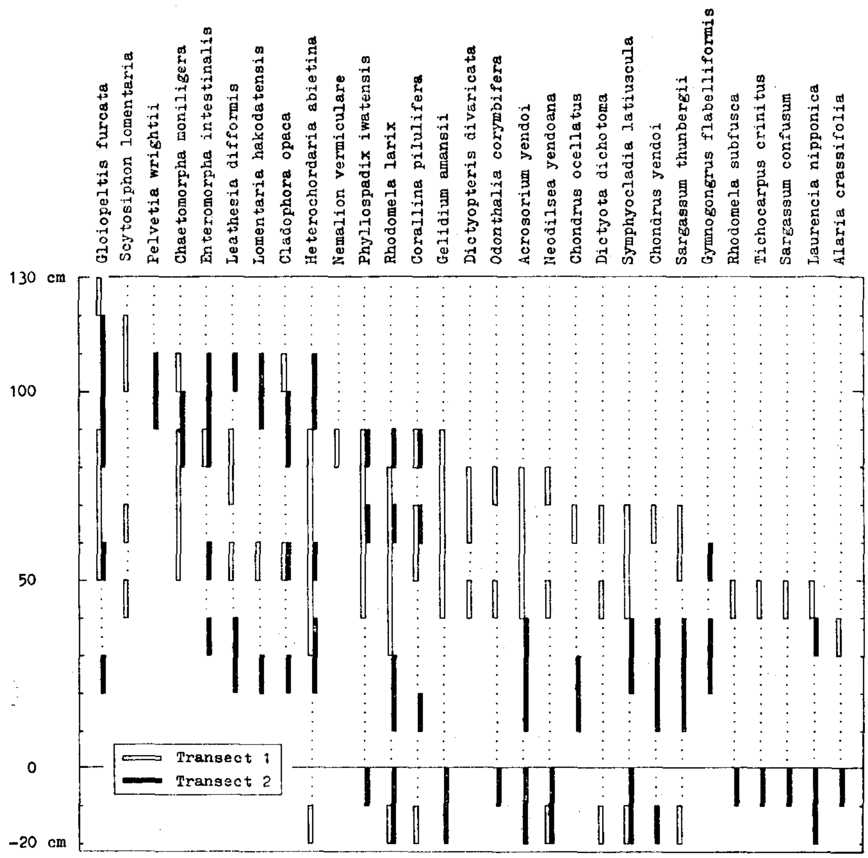

Fig. 9. A diagram showing vertical distribution of major species along Transects 1 and 2.

along Transect 1. This is clearly due to their occurrence in the first tide pool. Except for those occurrences, *Chaetomorpha moniligera* and *Cladophora opaca* also appear at higher places along Transect 2 than along Transect 1. Thus, six species appear higher along Transect 2 than Transect 1 within the seven species which occur more than 90 cm above the datum level and are distributed along both transects. Only one, *Gloiopeltis furcata*, appears at a higher place along Transect 1 than Transect 2. This is probably due to wave action. On most days at Benten-Jima, the waves were stronger on the coast where Transect 2 is located than near Transect 1. The direction of the wind at Usujiri was NW or W on 219 days in 1967 (observed by the Usujiri Branch of Minami-Kayabe Town Office). The reason for the appearance of *Gloiopeltis furcata* at a higher level along Transect 1 is not clear now.

Gelidium amansii and all the species enumerated on the right hand side of it in Fig. 9, except for a few sepcies which occur only along one transect, appear at much higher levels along Transect 1 than they do along Transect 2. The reason seems to be the presence of a large tide pool (Fig. 4) along Transect 1. Most species in this pool are, in a sense, invaders from the lower littoral or sublittoral regions. Having arrived by chance, they seem to remain because they can grow here and nothing has as yet killed or removed them. This tide pool, however, does not seem to be large enough for *Alaria crassifolia.* Although that species was not found in the tide pool between 32 and 43 meters, a few thalli were distributed at Station 15 which is located at the outermost limit of Transect 1. At Station 15, waves often wash over the rocks.

The third group of plants, comprising *Phyllospadix iwatensis*, *Rhodomela larix* and *Corallina pilulifera*, is found between the above two groups in Fig. 9. This group seems to grow in the depressions, even at higher levels (Fig. 7). The three species are found at Station 2 as well as Station 5, both of which are (Fig. 6) in a high level depressions along Transect 2. Although *Rhodomela larix* appears at a little higher level than the others along Transect 2 (Fig. 9), all of them would probably grow in zones up to the 80–90 cm level, if the substratum had suitable depressions in it.

Along Transect 3, algal zonation is much clearer than on the other transects. There is no essential difference in the optimum height of most species, whether the substratum is vertical or sloping. However, *Acrosorium yendoi* occurs much lower along Transect 3 among the species which occur along the three transects.

Table 4. Calculation of FICC (the example of Station 6 and Station 9 along Transect 1 is used). See Fig. 4 is the source of values for each species.

Species		Frequency			
		Maldistributed at St. 6	Common		Maldistributed at St. 9
			St. 6	St. 9	
Chaetomorpha moniligera	(Cm)	36			
Dictyota dichotoma	(Dd)				4
Leathesia difformis	(Ld)	20			
Heterochordaria abietina	(Ha)		32	44	
Sargassum thunbergii	(St)				12
Gelidium amansii	(Ga)				4
Gloiopletis furcata	(Gf)		88	12	
Chondrus ocellatus	(Co)				4
Chondrus yendoi	(Cy)				8
Acrosrium yendoi	(Ay)				4
Symphyocladia latiuscula	(Sy)				4
Rhodomela larix	(Rl)				72
Total		A: 56	B: 176		C: 112

FICC = 100B/(2A+B+2C) = 34. Note this value, thus, is that recorded in Table 5 for the relationship, FICC, between the communities in these two stations.

It appears below -170 cm along Transet 3, while it appears between -20 and 80 cm along the other two. The reason could be due to light intensity or desiccation. This species is usually found below large bushy thalli, viz. *Sargassum thunbergii*, along Transects 1 and 2. Such taller thalli might keep moisture for *Acrosorium* to persist during the aerial exposure periods. Moreover, the former could protect the latter against direct sunlight. Along Transect 3, however, there are no thalli like *Sargassum* and accordingly only *Acrosorium* grows lower. *Alaria crassifolia* and *Gelidium amansii* likewise grow at much lower levels along Transect 3 than along the other two transects, but the reason is not clear now.

The absence of algal thalli below -190 cm level could be explained by the variability in the height of the sand which sometimes covered the lowermost levels.

b) The algal community groups. Algal communities at the stations along Transects 1 and 2 are compared using FICC (= Frequency index community

Table 5. Grouping of the algal communities along Transects 1 and 2, according to FICC (FICC values more than 50 are shown by boldface). The transect number appears first in the column headings followed by the station number.

Transect & Station	1-4	2-1	2-3	2-9	2-4	1-5	1-6	2-7	2-8	2-10	2-6	1-13	2-2	1-9	2-13	1-12	2-11	2-12	1-7	1-14	2-16	1-15	2-5	1-10	2-17	2-14	2-15	1-8	1-11
1 - 4																													
2 - 1	**100**								Group A																				
2 - 3	**100**	**100**																											
2 - 9	**100**	**100**	**100**																										
2 - 4	**92**	**92**	**93**	**93**																									
1 - 5	**69**	**67**	**69**	**69**	**66**																								
1 - 6	**51**	48	**52**	**51**	**50**	**98**																							
2 - 7	43	43	46	45	46	**55**	**60**																						
2 - 8	38	36	39	39	43	**50**	**53**	**84**																					
2 - 10	41	39	42	41	46	**59**	**52**	**63**	**83**																				
2 - 6	39	36	40	39	46	**55**	43	35	**58**	45																			
1 - 13	25	34	40	39	38	**55**	45	**54**	**65**	**79**	40																		
2 - 2	33	30	34	27	32	**74**	33	26	39	31	**73**	41																	
1 - 9	25	22	28	27	26	39	34	28	30	36	14	24	27																
2 - 13	22	20	23	23	23	33	30	25	26	42	19	42	15	**76**					Group B										
1 - 12	20	17	22	20	23	46	41	29	32	30	32	35	**58**	**58**	48														
2 - 11	15	13	16	16	24	42	43	25	37	41	16	34	12	**72**	**54**	**58**													
2 - 12	0	0	0	0	0	18	19	17	23	34	4	29	2	**53**	**74**	29	**63**												
1 - 7	0	0	0	0	0	13	15	5	13	13	22	18	**50**	**51**	40	48	**55**	40											
1 - 14	0	0	0	0	0	13	12	8	9	15	5	16	31	**79**	**57**	**56**	**66**	**54**	**56**										
2 - 16	0	0	0	0	0	**52**	0	0	0	0	8	7	24	**54**	44	30	26	30	34	**61**									
1 - 15	0	0	0	0	0	17	18	10	13	23	0	26	7	**57**	18	33	34	22	30	47	12								
2 - 5	0	0	0	0	0	6	0	0	0	0	9	20	**67**	37	0	54	14	0	**60**	35	28	24							
1 - 10	0	0	0	0	0	0	0	0	0	0	5	15	14	30	6	27	14	7	16	16	6	4	25						
2 - 17	0	0	0	0	0	0	0	0	0	0	0	13	22	28	13	33	13	9	26	46	29	13	42	34				Group C	
2 - 14	0	0	0	0	0	0	0	0	0	0	6	12	18	24	13	36	7	6	16	25	21	7	27	**66**	**63**				
2 - 15	0	0	0	0	0	0	0	0	0	0	0	30	22	28	8	41	7	4	25	19	15	2	41	**68**	**54**	**68**			
1 - 8	0	0	0	0	0	0	0	0	0	0	0	8	44	37	17	38	14	1	45	36	22	26	**62**	**50**	**80**	**57**	**72**		
1 - 11	0	0	0	0	0	5	7	3	5	10	0	17	20	49	27	46	33	19	41	**53**	25	30	40	**51**	**64**	**64**	**63**	**66**	

Table 6. Calculation of FIIC (the example of *Sargassum thunbergii* and *Chondrus yendoi* is used). The values are from Figs. 4 and 6.

Transect & Station	St only	Coexistent		Cy only
		St	Cy	
1- 7	12			
1- 9		12	8	
1-12	8			
1-14		12	16	
2-11		4	12	
2-12		60	36	
2-13		56	4	
2-16		44	48	
2-17				4
Total	A:20	B:312		C:4

St: *Sargassum thunbergii*. Cy: *Chondrus yenodi*.
FIIC = 100B/(2A+B+2C) = 87. Such values for each species pair were used to form Table 7.

Table 7. Grouping of elevational indicator species according to FIIC. Boldface shows that the FIIC is more than 50 and italics more than 25. The calculation method for the index values for FIIC is given in Table 6.

Species	Gf	Ei	Cl	Ld	Lh	Cy	Gy	St	Dd	Tc	Rs	Sc	Ny	Pi	Oc	Ga
Gloiopeltis furcata		Group H														
Enteromorpha intestinalis	*29*															
Cladophora opaca	24	*49*														
Leathesia difformis	20	8	23													
Lomentaria hakodatensis	10	*28*	*49*	*38*												
Chondrus yendoi	3	8	12	20	6		Group M									
Gymnogongrus flabelliformis	7	23	4	13	0	*39*										
Sargassum thunbergii	6	10	9	22	9	**87**	**50**									
Dictyota dichotoma	5	9	23	*34*	20	**51**	*35*	**69**								
Tichocarpus crinitus	0	0	0	0	0	0	0	0	8			Group L				
Rhodomela subfusca	0	0	0	0	0	0	0	0	8	**100**						
Sargassum confusum	0	0	0	0	0	0	0	0	16	*47*	*49*					
Neodilsea yendoana	0	0	0	0	0	24	0	5	5	16	18	8				
Phyllospadix iwatensis	4	3	2	6	6	6	0	4	8	19	20	*36*	*36*			
Odonthalia corymbifera	0	0	0	0	0	0	0	0	9	**79**	**80**	**81**	*28*	*49*		
Gelidium amansii	2	1	2	6	6	4	0	4	17	*48*	*49*	**80**	*30*	**76**	**88**	

coefficient). Table 4 shows the method using the frequencies observed for each species. FICC increases toward 100 in proportion to the similarity between the two communities .If there are no common species, FICC is zero. The results are arranged according to their FICC, i.e. similarity, in Table 5. The communities can be divided into the following three groups on this basis:

Table 8. Calculation of the community characterization by using an elevational indicator species (this sample uses values for frequency from Station 9 on Transect 1 in Fig. 4).

Species with frequency		Frequency in each group		
		Group H	Group M	Group L
Rhodomela larix	72			
Heterochordaria abietina	44			
Sargassum thunbergii	12		12	
Gloiopletis furcata	12	12		
Chondrus yendoi	8		8	
Dictyota dichotoma	4		4	
Symphyocladia latiuscula	4			
Acrosorium yendoi	4			
Gelidium amansii	4			4
Chondrus ocellatus	4			
Total		12	24	4

The above community, as physically included in the quadrat at Station 9, is represented by the formula "12H+24M+4L".

Group A: *Transect 1* – Stations 4, 5, 6 and 13; *Transect 2* – Stations 1, 3, 4, 6, 7, 8, 9 and 10.

Group B: *Transect 1* – Stations 7, 9, 12 and 14; *Transect 2* — Stations 11, 12, and 13.

Group C: *Transect 1* – Stations 8, 10 and 11; *Transect 2* – Stations 14, 15 and 17.

All communties in any one of these three groups would have a somewhat common composition. The interspecific correlation according to habitat, FIIC (=Frequency index interspecific coefficient) is determined from the frequencies (=F) for indicator species as shown in Table 6. Species which show a close vertical distributional, or elevational, relationship with other species are selected as the indicator species. A few species which do not seem to represent distribution according to elevation are rejected. *Rhodomela larix* and *Heterochordaria abietina*, for example, are rejected because their distributions are too wide to be useful. Sixteen species are shown in Table 7 as elevation indicator species. *Pelvetia wrightii* and *Nemalion vermiculare* appear along one transect and not along the other. Therefore, their FIIC is not large. Both species, however, ought to be height indicator species. Including these two, the frequencies of the following eighteen species are used (Table 8) to characterize each community:

Group H: *Enteromorpha intestinalis, Cladophora opaca, Leathesia difformis, Pelvetia wrightii, Nemalion vermiculare, Gloiopeltis furcata* and *Lomentaria hakodatensis.*

Group M: *Dictyota dichotoma, Sargassum thunbergii, Chondrus yendoi* and *Gymnogongrus flabelliformis.*

Group L: *Sargassum confusum, Gelidium amansii, Neodilsea yendoana,*

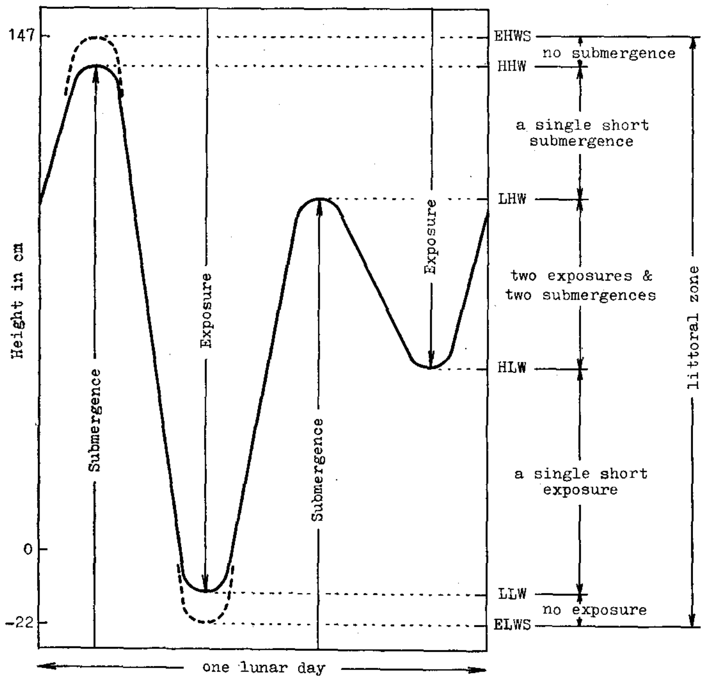

Fig. 10. A diagram showing tide movement and frequencies of both exposure and submergence in one lunar day.

Tichocarpus crinitus, Rhodomela subfusca, Odonthalia corymbifera and *Phyllospadix iwatensis.*

In this way the tendencies of all the communities as restricted by their quadrat boundaries are shown by the following formulae:

Group A: *Transect 1* – Station 4 (92H+OM+OL), Station 5 (116H+OM+OL), Station 6 (108H+OM+OL) and Station 13 (100H+OM+8L); *Transect 2* – Station 1 (76H+OM+OL), Station 3 (100H+OM+OL), Station 4 (108H+OM+OL), Station 8 (212H+OM+OL), Station 9 (96H+OM+OL) and Station 10 (148H+OM+OL).

Group B: *Transect 1* – Station 7 (OH+40M+4L), Station 9 (12H+24M+4L), Station 12 (56H+8M+24L) and Station 14 (OH+36M+16L); *Transect 2* – Station 11 (64H+78M+OL), Station 12 (20H+172M+OL) and Station 13 (32H+112M+OL).

Group C: *Transect 1*– Station 8 (OH+OM+52L), Station 10 (OH+16M+184L) and Station 11 (OH+OM+76L); *Transect 2* – Station 14 (OH+OM+124L), Station 15 (OH+OM+152L) and Station 17 (OH+4M+104L).

Transect 1 – Station 15's formula (OH+OM+OL) is not clear. Transect 2 – Station 2 seems to be a mixture of higher and lower characteristics (36H+OM+

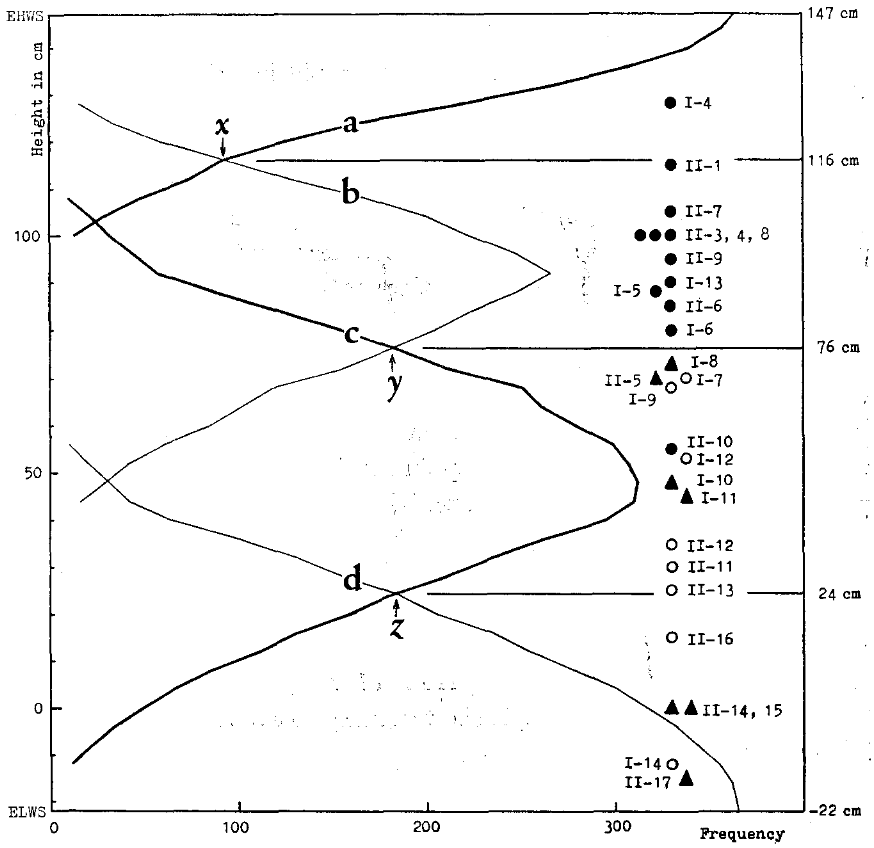

Fig. 11. Four subzones separated from one another at the levels of the three intersecting points (x, y and z) of curves a, b, c and d. Curve a: frequency during the year of each height above the daily HHW. Curve b: frequency of each height between the daily LHW and HLW. Curve c: frequency of each height between the daily HLW and LLW. Curve d: frequency of each height below the daily LLW. The a, b, c and d were determined for the period of July 11, 1967, and July 10, 1968. On the right hand side, stations along Transects 1 and 2 are enumerated according to their heights. A black spot denotes "Group A" communities, a white spot "Group B", and black triangle "Group C", each as of July, 1968.

20L). Transect 2 - Station 5 (OH+OM+4OL) and Station 16 (OH+92M+OL) are members of Group C and of Group B, respectively.

Although none of these three algal community groups is distinguished by the occurrence of some one indicator species, the existence of the three is substantiated by this comparison of algal composition. The reason for their existence might be due to tide factors, the unevenness of the rock surface or other factors. These will be discussed later.

c) The influence of the critical tide factors. Among the environmental factors that influence an algal community group, the tide factor is very important. Many phycologists have discussed the relationship between vertical algal distribution and tide factors. Doty (1946), for example in describing the nature of critical tide factors, pointed out their correlation with the vertical distribution of marine algae and other organisms along the Pacific Coast of North America. He emphasized their elevational extremes and durational features.

In Japan, Katada (1952) pointed out that we should attach importance to frequencies both of exposure and submergence rather than to total hours of exposure or submergence. Diurnal inequality of tides produces HHW, LHW, HLW and LLW, respectively. Where there are semi-diurnal mixed tides, there are (Fig. 10) two exposures as well as two submergences daily. So, HHW, LHW, HLW and LLW can be regarded as possible boundary levels in the environment for organisms on that day. However, the elevation of these tidal features varies with the fortnightly periodic shifts between neap and spring tides. Thus the above idea of frequency must be added to this otherwise oversimplified scheme. To illustrate this point, Fig. 11 has been prepared according to the tides at Usujiri between July 11, 1967, and July 10, 1968. Katada's subzones are limited at the three intersecting points, x, y and z, which Fig. 11 displays as EHWS-x, x-y, y-z and z-ELWS. Thus each subzone might be characterized by the following conditions:

EHWS-x (between the 147 and 116 cm levels): total of both days without submergence and those with a single short submergence are moe frequent than days with other tidal conditions*.

x-y (between the 116 and 76 cm levels): days with both two exposures and two submergences are more frequent than days with other tidal conditions.

y-z (between the 76 and 24 cm levels): days with a single short exposure are more frequent than days with other tidal conditions.

z-ELWS (between the 24 and -22 cm levels): days without exposure are more frequent than days with other tidal conditions.

The tentative distribution of each algal community is shown along the right hand side of Fig. 11. A break between the "A-group" and the other is seen at 76 cm above the datum level. Eleven of the twelve communities in Group A are distributed above that level, with Station 10 at 55 cm above the datum level along Transect 2 being the only exception. A break at the 24 cm level is not very clear, but the 76–24 cm zone seems to be the Group B zone, with Station 14 along Transect 1 and Station 16 along Transect 2 being exceptions. Also, a Group

* This subzone is divisible into two, viz.: 1) Between the EHWS and HHW levels, as seen in Fig. 10, days without submergence are more frequent than days with other tidal conditions; and 2) between the HHW and LHW levels, as seen in Fig. 10, days with a single short submergence are more frequent than days with other tidal conditions. The above two were combined by Katada because the HHW and LHW levels are relatively close to one another in Japan.

C zone appears, with some exceptions, below 24 cm above the datum level. Most of the exceptions are found in a tide pool (Transect 1 – Stations 8, 10 and 11) or in a rock depression (Transect 2 – Station 5).

Katada (1952) proposed his subzones on the basis of tide level. We support his idea on the basis of the existence of our three groups of algal communities which are nicely applicable to his subzones.

The distribution of the three groups of algal communities, however, is restricted not only by tide level, but also by the rock configuration. Station 5 along Transect 2, for example, is located above the datum level and is, thus, much higher than most of the stations in Group C. However, the communities at Station 5 ought to be in Group C. The reason that it is not at Group C zone in height seems to be that Station 5 is in a depression. This is made clearer by Figs. 5 and 7. If there is a tide pool, this tendency is evident in the distribution of the communities at Ststions 8, 10 and 11 along Transect 1. Thus we must consider the irregularities of the rock as well as the tide levels in the course of algal phytosociology work.

We did not compare Stations 1, 2 and 3 along Transect 1 with the others because their plant communities are essentially different. At Stations 1 and 2, a few species such as *Chaetomorpha moniligera* grow. In the spring, other species appear such as *Dumontia simplex* and *Rhodomela subfusca*. However, only a single species, *Scytosiphon lomentaria*, was observed at Station 3. In an unfavourable environment, the outburst of a single or a few species is often observed. In the tide pools, the water temperature can be more than 30°C in summer and below freezing point in the winter. Salinity is variable due to rain and the melting of snow. It would be high if flooded during high tide periods and perhaps nearly fresh water during the ebb tide. Although the conditions are not favourable for most species, the above three and a few others can live under such circumstances. They occupy most of the substratum during their growth period. The dense cover of *Scytosiphon lomentaria* observed to persist at Station 3 up until July is an example of this.

2. Coverage

a) Comparison of algal coverage along three transects. The coverages of the major species (more than 1% in all of the studied areas along each transect) and the total for each transect is shown in Fig. 12. Along Transect 3, the coverages above -20 cm are used. In total coverage, Transect 2 is seen to be the largest (47.1%) among the three. Transect 1 comes next (32.7%) and the smallest is Transect 3 (22.7%).

The most abundant single species in a transect is *Ptilota pectinata* which is along Transect 3 (14.8%). This species does not occur along the other two transects. Next in abundance is *Rhodomela larix* found along Transect 1 (14.6%), which also occurs along Transect 2 (5.6%). The third is *Gloiopeltis furcata* from Transect

2 (11.5%), which also occurs along Transect 1 (4.7%). Although the optimum zone for *Gloiopeltis furcata* seems to be large, this species grows only on rocks or pebbles which, at least for a short time, appear above water every day. This species on Transect 2 does not occur below 24 cm above the datum level. In a tide pool, there is no exposure even at ebb tide period. This must be the reason *Gloiopeltis furcata* is abundant along Transect 2 rather than along Transect 1 which has a large tide pool at the optimum zone for this species. The abundance of *Rhodomela larix* along Transect 1 can be explained also by the presence of a pool since it seems to have tendencies opposite those of *Gloiopeltis furcata* in respect to elevation. *Heterochordaria abietina* (7.2%) and *Phyllosphadix iwatensis* (6.9%) are both found along Transect 2 and their coverages along Transect 1 are much smaller 2.5 and 1.6%, respectively). *Heterochondaria abietina* tends toward Group M, but is rejected because its distribution is so large (cf. p. 55). Its optimum habitat is absent along Transect 1 because of a lare tide pool, however, it is extensive along Transect 2. The reason for the abundance of *Phyllospadix iwatensis* is not clear. *Ulva pertusa* is found along Transect 3 (4.5%) and along the other two only in trace amounts. *Sargassum thunbergii* is found along Transect 2 (2.9%), is absent along Transect 3 and is only in trace amounts along Transect 1. The abundance of *Sargassum thunbergii* and *Chondrus yendoi* (1.4%) along Transect 2 can be interpreted in the same way as the abundance of *Heterochordaria abietina* along the same transect. *Scytosiphon lomentaria* is noted along Transect 1 (2.8%) but is lacking along the other two. This can be explained by the presence of the second tide pool along Transect 1.

There are twenty-seven common species found in Transects 1 and 2. Four are peculiar to Transect 1 and six to Transect 2. Most of the latter are not abundant along either transect. Thus, the communities of both transects are similar. Of the ten species occurring above the −20 cm level of Transect 3, eight species are present along Transect 1 or 2. The remaining two, *Ptilota pectinata* and *Rhodymenia pertusa,* are peculiar to Transect 3. *Rhodymenia pertusa* is not abundant above -20 cm while *Ptilota pectinata* is characteristically abundant and is the single dominant species (cf. p. 61). One of the definite differences between the communities of the vertical transect (Transect 3) and those of the natural rocky platform (Transects 1 and 2) is the presence or absence of *Ptilota pectinata*. *Rhodomela larix* and *Gloiopeltis furcata* are found abundantly along Transects 1 and 2, but lacking along the vertical transect. This is another major difference between their communities.

Taniguti (1961) studied the algal communities at several places in Hokkaido. As far as we know, *Rhodomela larix* is growing abundantly all around Hokkaido, but his results contain only a few records of this species. That he studied vertical or steep rock surfaces is easily seen by reviewing his methods and Figs. 1 and 2 in his paper, but otherwise would have been suspected from the above results.

Gloiopeltis furcata seems to have other factors regulating its distribution, other than the slope of the substratum. This phenomenon will be discussed in the future, after studies have been made along other coasts.

The FICC relationships between the three transects, each taken as a single community, are as follows:

Transects 1 and 2: 83.
Transects 1 and 3: 25.
Transects 2 and 3: 23.

b) The dominant and subdominant species. Along Transect 1, the dominant and subdominant species can be selected from dominance in terms of coverage. *Rhodomela larix* (C=14.6%) and *Gloiopeltis furcata* (C=4.7%), with a total coverage of 19.3%, provide more than half of the total for all algae along the transect (32.7%). The above two species are then considered the dominant species on Transect 1. If we add the coverages of *Scytosiphon lomentaria* (2.8%) and *Heterochordaria abietina* (2.5%) to the above (19.3%), the total becomes 24.6%. This is more than 75% (three-fourths) of the total for all algae along the transect. The latter two are, thus, considered the subdominant species. Perhaps the number of dominant and subdominant species could be used as an indicator of a community's stability or other tendencies after more studies have been made of this point. The dominant (boldface) and subdominant species of the three transects are:

Transect 1.
1. ***Rhodomela larix***
2. ***Gloiopeltis furcata***
3. *Scytosiphon lomentaria*
4. *Heterochordaria abietina*

Transect 2.
1. ***Gloiopeltis furcata***
2. ***Heterochordaria abietina***
3. ***Phyllospadix iwatensis***
4. *Rhodomela larix*
5. *Sargassum thunbergii*
6. *Chondrus yendoi*

Transect 3.
1. ***Ptilota pectinata***
2. *Ulva pertusa*

c) The relationship between coverage and standing crop. The wet or dry weight of a certain species in a 50×50 cm quadrat is regulated by its coverage. Of course, this regulation will vary according to the season.

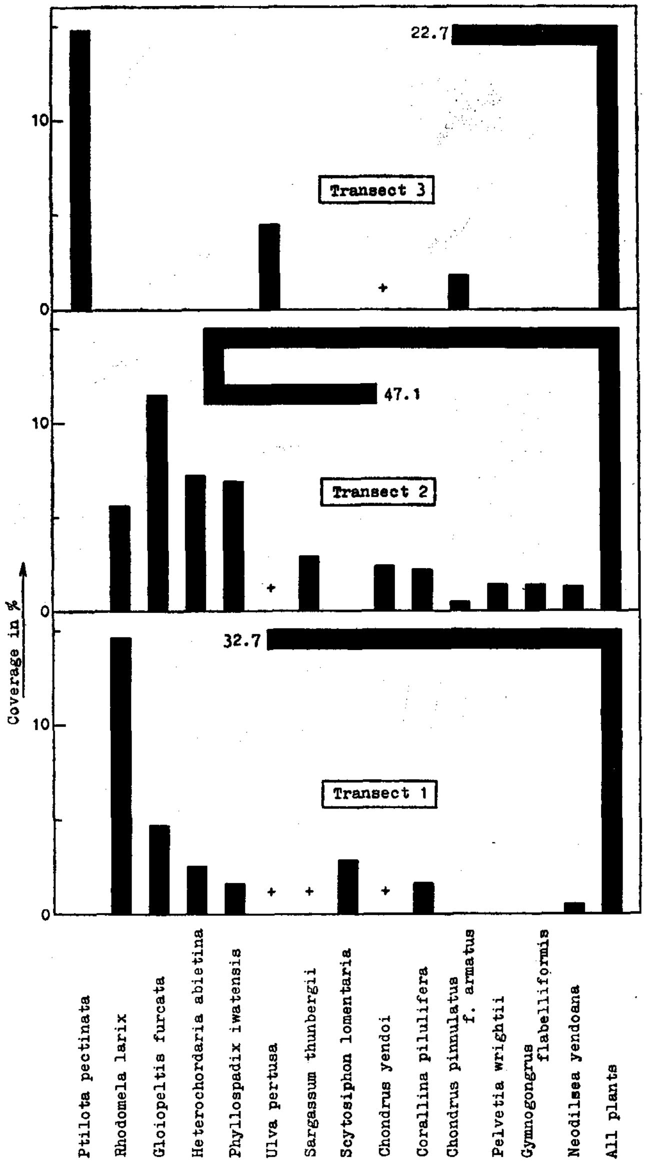

Fig. 12. An illustration of the contrast in algal coverage along the three transects on July 10–12, 1968.

On July 10, 1968, the dry weight to coverage ratio of *Rhodomela larix* at four stations was 3.2, 3.3, 3.4 and 4.2 (gram/coverage in %), respectively (Table 1). Using the average of these index values, 3.5±1.2, we can predict the dry weight of *Rhodomela larix* in the belt along the 50 cm wide Transect 1 (15 m^2) to be about 3±1 kg. It would be about 15 kg in wet weight, because the "wet weight/ dry weight" ratio is about 5.

Using the above method, the dry weight of all plants in the 50 cm width of Transect 1 can be assumed to be about 11 kg, which would be 48 kg in wet weight. The mean dry and wet weights in one square meter would be about 0.7 kg/m^2 and 3.2 kg/m^2, respectively, since the total area is 15 square meters. The mean dry and wet weights of plants for the five stations in which the standing crop was studied are 1.5 kg/m^2 and 6.4 kg/m^2, respectively.

3. Seasonal variation of the algal commmunity

The total coverage was at its maximum on June 14 (43.3%), and minimum on December 18 (12.0%). Then it increased again toward May 4, 1969 (22.4%) (Table 2).

Among the species occurring along Transect 1, *Rhodomela larix* and *Gloiopeltis furcata* appear as dominant species in most of the observations during the study period. The former seems to be a representative inhabitant of the lower area as well as the large tide pool and the latter to be that of a higher area. Few other species occur as dominant species of the transect in some seasons. Their seasonal variation, whether they are dominant or subdominant, is shown by boldface or italic type, respectively (Table 2).

Most of the species fall into one of three kinds according to their vegetative growth period. These groups are tentatively named spring type, summer type and autumn type, respectively. Those whose coverage (or frequency, if the coverage is not clear) begins to increase in or after winter and show a maximum before or in summer, are called the spring type. A species whose coverage (or frequency, if the coverage is not clear) begins to increase in or after summer and show a maximum before or in winter, is called the autumn type. The few species which appear only during the short summer period are called the summer type. The species of the last type could be combined with one of the other two, but for now, we propose to recognize three types. The typical members of the three groups and their months of maximum coverage (or frequency) are therefore:

Spring type: February – *Dictyopteris divaricata*; April – *Dumontia simplex*; May – *Monostroma angicava, Scytosiphon lomentaria, Colpomenia bullosa, Bangia fusco-purpurea* and *Laurencia nipponica* (not very clear); June – *Enteromorpha intestinalis, Leathesia diffromis, Heterochordaria abietina, Gloiopeltis furcata, Porphyra yezoensis, Gelidium amansii, Rhodomela subfusca, Sargassum thunbergii* (also in July) and *Cladophora opaca* (not very clear); July – *Sargassum confusum, Rhodomela larix* and *Odonthalia corymbifera*; August – *Phyllospadix iwatensis*.

Summer type: July – *Chaetomorpha moniligera*; August – *Nemalion vermiculare*.

Autumn type: November – *Dictyota dichotoma* and *Lomentaria hakodatensis* (not very clear); December – *Corallina pilulifera*; February – *Chondria crassicaulis*.

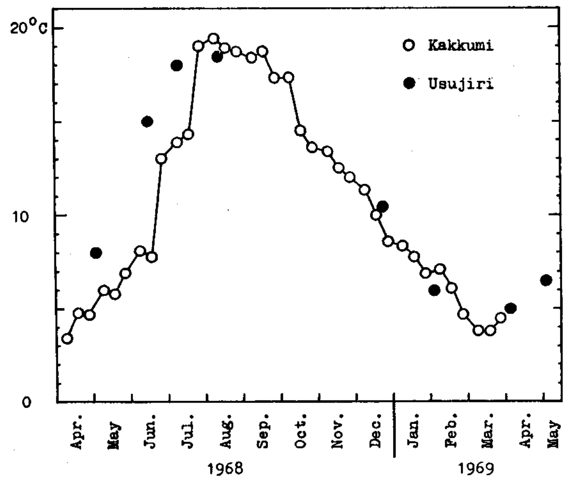

Fig. 13. Seasonal change in surface water temperature at Kakkumi and Usujiri, during the period of the present algal vegetation study.

There could be some errors in the above list, especially in respect to the month of maximum growth. *Porphyra yezoensis*, for example, so far as we know, is at maximum in a much earlier month than June in Southern Hokkaido. This would be especially a likely error for annuals. Although there are such errors, we believe that the study gives us a general view of the seasonal variation of each species. There are some examples of autecological knowledge on a few of the species contributed by previous workers. A few of them are as follows:

1) Tokida, Masaki & Yabu (1953) studied the rhizoids of *Dictyopteris divaricata* from Oshoro Bay, Hokkaido. They cultured them and found they give rise to numerous young leafy thalli in the autumn. After that time, young thalli in the same condition as those cultured were found in nature. They concluded that the species had the ability to propagate vegetatively in nature this way. They also noted that the thalli in nature were 0.8–1.0 mm long on October 8, 2–3 mm long on December 13, and 5 cm in mean length (a maximum of 9 cm) by February 18. Thus, the young thalli would be considered as begining to grow in autumn and we recorded this as well (Table 2) at Usujiri where its maximum coverage was recorded in February. However, since light and temperature are increasing in February through the spring period and our May and April measurements of coverage are also high, we feel this is a spring species.

2) Tokida, Komatsu & Kaneko (1964) reported that *Dumontia simplex* is an annual plant. At Oshoro Bay, Hokkaido, it grew from October through late June or, sometimes through the beginning of July. It began to give rise to reproductive organs in November and fully grown thalli were observed from December through February. At Moheji, near Hakodate, Hokkaido, mature thalli were observed from

early December onwards. Most of them were dead in late June. This autecological information agrees well with our results from Usujiri.

Altogether, there are twenty spring type, two summer type and four autumn type species. Species which appear dominant along the transect at least once a year are all of the spring type. Species of this kind increase their coverage following the winter period. It is not clear when their microscopic growth would begin except for *Dictyopteris divaricata* as discussed above. But the beginning of macroscopic growth after winter seems to be common in most algal species. Favourable conditions for the growth of most algal species would be in the increasing temperature and light of spring. Also, as is well known, the spring growth of diatoms is greater than that in autumn.

Although the frequency and coverage by each alga varies seasonally as discussed above, there is no essential variation in the distributional pattern along the transect. This phenomenon shows that we can compare results collected from different places at different seasons.

Seasonal change of the surface water temperature at Usujiri, during the study, was but fragmentarily recorded. The records at Kakkumi, located 4 km southwest of Usujiri, are shown in Fig. 13 (through the kindness of Dr. Y. Hasegawa of the Hokkaido Regional Fisheries Research Laboratory) together with our records.

V. List of species

Species which occurred along the three transects on Usujiri Benten-Jima, and at least once a year, along Transect 1, are:

Chlorophyceae

1.	*Monostroma angicava* Kjellman	エゾヒトエグサ
2.	*Ulva pertusa* Kjellman	アナアオサ
3.	*Enteromorpha intestinalis* (Linnaeus) Link	ボウアオノリ
4.	*Cladophora opaca* Sakai	ツヤナシシオグサ
5.	*Chaetomorpha moniligera* Kjellman	タマジュズモ

Phaeophyceae

6.	*Dictyota dichotoma* (Hudson) Lamouroux	アミジグサ
7.	*Dictyopteris divaricata* (Okamura) Okamura	エゾヤハズ
8.	*Leathesia difformis* (Linnaeus) Areschoug	ネバリモ
9.	*Heterochordaria abietina* (Ruprecht) Setchell and Gardner	マツモ
10.	*Scytosiphon lomentaria* (Lyngbye) J. Agardh	カヤモノリ
11.	*Colpomenia sinuosa* (Roth) Derbes and Solier	フクロノリ
12.	*Colpomenia bullosa* (Saunders) Yamada	ワタモ

13.	*Laminaria japonica* Areschoug	マコンブ
14.	*Costaria costata* (Turner) Saunders	スジメ
15.	*Undaria pinnatifida* (Harvey) Suringar	ワカメ
16.	*Alaria crassifolia* Kjellman	チガイソ
17.	*Pelvetia wrightii* (Harvey) Yendo	エゾイシゲ
18.	*Sargassum confusum* Agardh	フシスジモク
19.	*Sargassum thunbergii* (Mertens) O. Kuntze	ウミトラノオ

Rhodophyceae

20.	*Bangia fusco-purpurea* (Dillwyn) Lyngbye	ウシケノリ
21.	*Porphyra yezoensis* Ueda	スサビノリ
22.	*Nemalion vermiculare* Suringar	ウミゾウメン
23.	*Bonnemaisonia hamifera* Hariot	カギケノリ
24.	*Gelidium amansii* Lamouroux	マクサ
25.	*Dumonita simplex* Cotton	ヘラリウモン
26.	*Neodilsea yendoana* Tokida	アカバ
27.	*Corallina pilulifera* Postels and Ruprecht	ピリヒバ
28.	*Grateloupia filicina* (Wulfen) J. Agardh	ムカデノリ
29.	*Grateloupia livida* (Harvey) Yamada	ヒラムカデ
30.	*Grateloupia divaricata* Okamura	カタノリ
31.	*Carpopeltis affinis* (Harvey) Okamura	マツノリ
32.	*Gloiopeltis furcata* Postels and Ruprecht	フクロフノリ
33.	*Tichocarpus crinitus* (Gmelin) Ruprecht	カレキグサ
34.	*Schizymenia dubyi* (Chauvin) J. Agardh	ベニスナゴ
35.	*Caulacanthus okamurai* Yamada	イソダンツウ
36.	*Gymnogongrus flabelliformis* Harvey	オキツノリ
37.	*Rhodoglossum japonicum* Mikami	アカバギンナンソウ
38.	*Chondrus ocellatus* Holmes	ツノマタ
39.	*Chondrus crispus* (Linnaeus) Stackhouse	トチャカ
40.	*Chondrus pinnulatus* (Harvey) Okamura f. *armatus* (Harvey) Yamada and Mikami	トゲツノマタ
41.	*Chondrus yendoi* Yamada and Mikami	エゾツノマタ
42.	*Rhodymenia pertusa* (Postels and Ruprecht) J. Agardh	アナダルス
43.	*Lomentaria hakodatensis* Yendo	コスジフシツナギ
44.	*Ptilota pectinata* (Gunnerus) Kjellman	クシベニヒバ
45.	*Ceramium japonicum* Okamura	ハネイギス
46.	*Ceramium kondoi* Yendo	イギス
47.	*Acrosorium yendoi* Yamada	ハイウスバノリ
48.	*Polysiphonia morrowii* Harvey	モロイトグサ
49.	*Polysiphonia urceolata* (Dillwyn) Greville	ショウジョウケノリ

50. *Chondria crassicualis* Harvey ユナ
51. *Laurencia nipponica* Yamada ウラソゾ
52. *Symphyocladia latiuscula* (Harvey) Yamada イソムラサキ
53. *Rhodomela larix* (Turner) Agardh フジマツモ
54. *Rhodomela subfusca* (Woodward) Agardh イトフジマツ
55. *Odonthalia corymbifera* (Gmelin) J. Agardh ハケサキノコギリヒバ

Phanerogamae

56. *Phyllospadix iwatensis* Makino スガモ

VI. Summary

Marine benthic algal phytosociology work was carried out in a littoral zone (as defined by T. & A. Stephenson, 1949), along three transects in different locations in Usujiri Benten-Jima, Hokkaido, July 10 to 12, 1968. Along one transect bathed by a relatively calm sea, the seasonal variations of the algal communities were observed between May 3, 1968 and May 4, 1969. The results obtained are summarized below:

1. The algal communities on a natural rocky slope are classified in three groups according to their species composition. These three groups are, as a rule, nicely relatable to the subzones recognized by Katada (1952) on the basis of tide factors. Although there are some exceptions, there is no essential difference between the algal zonation on a natural rocky slope and that on the lateral surface of a vertical substratum. So, it might be said that algal zonation is strongly regulated by tide factors.

2. Algal zonation is also influenced by wave action, rock surface irregularity, and by other organisms. Examples are: 1) The upper limit of the algal communities is usually regulated by the constancy and strength of wave action (see the upper commuities along Transect 2, which appear higher than those of Transect 1). 2) Rock depressions in a higher area seem to attract some species which are otherwise usually found in a lower area. *Rhodomela larix*, *Corallina pilulifera* and *Phyllopsadix iwatensis* are examples of this. They grow as high as 70–80 cm above the datum level. If a depression forms a tide pool, the tendency to move up is very clear. 3) Some species seem to attract others. For example, *Acrosorium yendoi* which normally grows on lower rocky slopes, seems to be attracted upwards by *Sargassum thunbergii* which grows higher up.

3. Certain algae can live in a seemingly unfavourable environment, such as a high tide pool. Those species usually occupy the substratum without any rival species (see the *Scytosiphon lomentaria* community at Station 3 along Transect 1).

4. *Ptilota pectinata* grows abundantly in the littoral zone of vertical

substrata, but never grows on a natural rocky slope. However, *Rhodomela larix*, *Gloiopeltis furcata* and *Phyllospadix iwatensis* which grow in abundance on the natural rocky slopes, never grow on the lateral sides of the vertical substrata.

5. Using the algal coverage, we defined dominant and subdominant species (see p.61). *Rhodomela larix*, *Gloiopeltis furcata*, *Heterochordaria abientina* and *Phyllospadix iwatensis* tend to become dominant on a natural rocky slope. Their order may change according to irregularity of the substratum or other factors. Only a single species, *Ptilota pectinata*, was dominant on vertical surfaces. The degree of dominance as well as of subdominance, both in respect to number and order of species, is possibly useful as a key to the tendencies within the communities or to their peculiarities of the environment.

6. Along Transect 1, the mean dry weight of the algal standing crop was calculated to be 0.7 kg (3.2 kg wet weight) per square meter.

7. The distributional pattern along the transect, facing the calm side (Transect 1), does not change essentially with the seasons. However, the frequency and coverage of each species vary. Total coverage was maximum on June 14, 1968 and at a minimum on December 18, 1968. After December, it increased again.

8. *Rhodomela larix* was constantly the dominant species on Transect 1, while *Gloiopeltis furcata* was another dominant species during every observation period except for that in August. The former seems to be characteristically the dominant inhabitant of the lower elevations and the latter that of the higher.

9. The maximum coverage of most species was present in June (9 spp.), May (5 spp.) or July (3 spp.). Twenty species, including the above 17, begin to increase their coverage in or after winter and achieve their maximum coverage as stated or in the summer. Such species are designated as being of the spring type. There are, thus, more spring type species than summer type or autumn type species.

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