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ECOLOGICAL DISTRIBUTION OF EPIPHYTIC HYDROZOA ON THE TSUCHIYA COAST NEAR THE MARINE BIOLOGICAL STATION OF ASAMUSHI[1)]

By

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Hydrozoa are very abundant in species and biomass in the vicinity of the Marine Biological Station of Asamushi. Studies on the life cycle and taxonomy of the various Hydrozoa have been done by many authors at the station and an ecological investigation was undertaken by Katô *et al.* (1961) on the distribution pattern of Hydrozoa on sargasso-algae.

There have been extensive works on the association between Bryozoa and algae in the region of Woods Hole (Rogick and Croasdale, 1949) and in British waters (Ryland, 1962). Ryland (1959a and b, 1962) suggested the important role of the positive selection of algae by bryozoan larvae in determining the distribution of these species on the shore, judging from the results of the field observations and his well designed experiments. However, there were no works dealing with the association between Hydrozoa and algae at least in Japan, although occasional descriptions are found in faunal and taxonomic papers (Yamada, 1950, 1959, etc.)

In the previous paper, the general observations on the association of Hydrozoa with various substrata (with special reference to algae) were reported and it was suggested that there is a suitable group of algae such as Sargassaceae as well as an opposite extreme like most Chlorophyta and several other algae that do not support the epiphytic animals, and moreover, the epiphytic Hydrozoa mostly show a high-degree of preference for given algae and consequently the distribution of these Hydrozoa on the shore must be in good accordance with that of their respective preferable alga (Nishihira, 1965).

The main purpose of the present work is to draw the actual figures of the ecological distribution of the epiphytic Hydrozoa along the Tsuchiya coast near the Marine Biological Station of Asamushi to check the previous conclusion and the assumption presented. It is attempted to know the hydrozoan fauna and how abundant they are, where they occur, and if possible why they show such distribution.

1) Contributions from the Marine Biological Station of Asamushi, Aomori Ken, No. 330

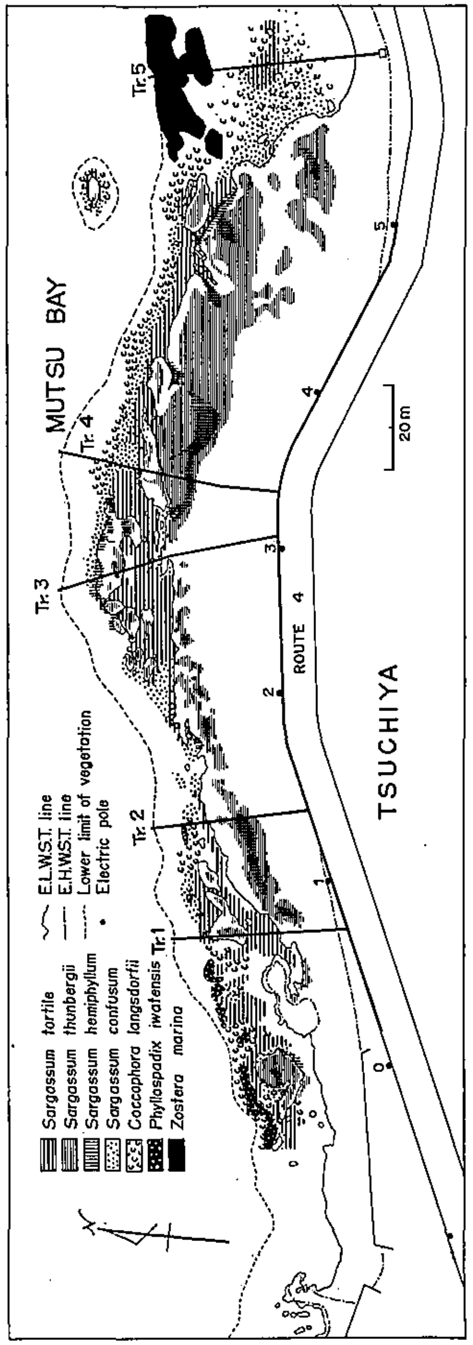

Fig. 1. The map of study area showing the distribution of the chief vegetation types and sampling traverses.

I express my thanks to Prof. Mutsuo Katô, Biological Institute of the Tôhoku University, for his interest in all aspects of the present study and his critical reading of the manuscript. My thanks are also due to Prof. Eturô Hirai and the staff members of the Marine Biological Station of Asamushi for their valuable criticism.

STUDY AREA

At the Tsuchiya coast an abrasion platform projects about 50m seawards and is almost entirely covered during high tide of the spring tides. There grow a variety of algae, among which the chief ones are those of the Sargassaceae, *Enteromorpha* spp. and *Ulva pertusa* (UP). The bed rock between the tide marks is in part covered by a dense carpet of *Sargassum thunbergii* (ST), while other parts support no vegetation but serve as the sites for the sessile invertebrates such as barnacles, *Balanus amphitrite albicostatus* and *Chthamarus challengerii*, and mussels as *Mytilus edulis* and *Septifer virgatus*. From the infralittoral fringe downward various algae are flourishing but from the seaward end of the platform outwards, the bottom is replaced by sand where no algal growth can be met, whereas in some places *Zostera marina* (ZM) is very luxuriant.

An approximate distribution of the chief vegetation types composed of Sargassaceae and Zosteraceae is shown in Fig. 1, which together shows the sampling traverses. *Sargassum tortile* (SO) grows in the rocky area infralittorally, especially in the part protected from waves by the rocks to some degree. It forms

the well developed, more or less pure, submerged forest. The characteristic region of *Sargassum confusum* (SF, previously designated as *S. fulvellum* in Nishihira, 1965) is formed where the bottom is sand with boulders around Traverse 5, and in the same situation a well developed *Coccophora langsdorfii* (CL) region appears. *Sargassum hemiphyllum* (SH) flourishes around the infralittoral fringe, while *S. thunbergii* grows midlittorally, especially in front of the electric poles 3, 4 and 5. *Zostera* forms a *Zostera* belt on the sandy bottom, whereas another plant of Zosteraceae, *Phyllospadix iwatensis* (PI), grows on the rocky area around the infralittoral fringe. Green alga, *Enteromorpha compressa* (EC), grows higher, in the midlittoral zone, than other algae except *S. thunbergii*, and forms the green area in front of the electric pole 1, and another green alga, *Ulva*, grows almost uniformly throughout the infralittoral rocky area.

Sixteen species of Hydrozoa, two of which belong to Athecata, were reported by Stechow and Uchida (1931) in the 'Report of the Biological Survey of Mutsu Bay.'

The Tsuchiya coast affords various kinds of bottom natures, well developed vegetations and a variety of Hydrozoa, which is the main reason for selecting the area for study.

The tidal range is about 1m, but this does not occur in one tide, since the highest high water is not proceeded or followed by the lowest low water there. The tide is semidiurnal. The general outline of the biological and physical environs along the coast of Asamushi and the vicinity is given by Hoshiai (1965).

METHODS EMPLOYED

Five traverses were set cutting the main vegetations, namely Traverse 1, 40m in length, commenced at the *Enteromorpha* region which was neighboured by *Ulva* and followed by the *S. tortile* forest; Traverse 2, about 40m in length, was a modification of the first; Traverse 3, 51m in length, was on the typical *S. tortile* region and *Mytilus* bed which was followed by *S. hemiphyllum*; Traverse 4, 50m in length, was put on the typical *S. thunbergii* bed which was followed by the *S. tortile* forest and by *Coccophora* successively; and the last, Traverse 5, 55m in length, was set on a sandy bottom, where *Zostera* appeared. All traverses start from the foot of the sea-wall and extend outwards in seaward direction. A quadrat ($50\times50cm^2$) was put at an interval of one meter on all traverses except Traverse 5, and the coverage and bottom nature were recorded with some notes about the sedentary animals such as barnacles, mussels, and snails. On Traverse 5, sampling was done at every two and a half meters using the same quadrat. A fourth of the algae in the quadrat was scraped off. The sampling period lasted about a month from mid-July to mid-August.

The samples collected were examined in the laboratory with an aid of a binocular dissecting microscope when necessary. Hydrozoa were identified, counted, and measured according to weeds and quadrat number. The estimation of the colony size was done according to Katô *et al.* (1961), who expressed the colony size by estimating the length of the algal thalli (stems or branches of *Sargassum*) on which the hydrorhiza adhered. It is obvious that this method does not always give accurate figures of the biomass when applied to the colonies attaching to various algae. Even when a biomass is far from identical with one another the figures are often similar even between the colonies of the same species. The age of the colony, life form of the algae, and the existence of other organisms of similar life form are the most influential factors causing such difficulty. It is possible, however, to get a general idea about the colony mass through this technique.

In comparing the abundance of Hydrozoa on the thalli, it is desirable to prove that all factors except the difference in algal species are the same, but in the open situation like a rocky shore the requirement may be hardly satisfied. It is rather convenient to treat the algal species together with the environmental factors which permit the alga to grow. Such a method may not present the exact positive figures of the preferability of an algal species itself. The influence of the environmental factors other than the alga itself can be analyzed by sampling various algae growing interminglingly at the same place and also by sampling the same algal species from various situations. The ecological factors considered here are the species of algae, tidal level and bottom nature. Comparison between algae as the substratum was done on the basis of fresh weight, which is not necessarily desirable because of a variety of life forms of algae. No method was available to compare the various algal species with one another on a common basis. The figures obtained by the method used show the general feature of the degree of association between the Hydrozoa and algae when corrected by the index of the surface area of the thalli. Colman (1940) compared the fauna inhabiting various algae in different tidal levels on the basis of algal weight.

RESULTS

I. GENERAL RELATION BETWEEN HYDROZOA AND WEEDS

The amounts of Hydrozoa (mm) and algae (g) are shown in Fig. 2, which shows that each traverse has a characteristic pattern in their distribution. Both figures seem to be correlated with each other with the exception on Traverse 5. On Traverse 1 and 2, large values of the correlation coefficient occur (0.782 and 0.746), and on 3 and 4 there are also significant values though somewhat smaller (0.418 and 0.527). On Traverse 5, correlation was not significant (0.179), and this may be attributed to the particular nature of the vegetation. It is noteworthy that there are several points where Hydrozoa do not appear in spite of the presence of sufficient algae as shown around point 10 on Traverse 1, around point 20 on Traverse 2, and on several points on Traverse 3 and 4. Here, it becomes necessary

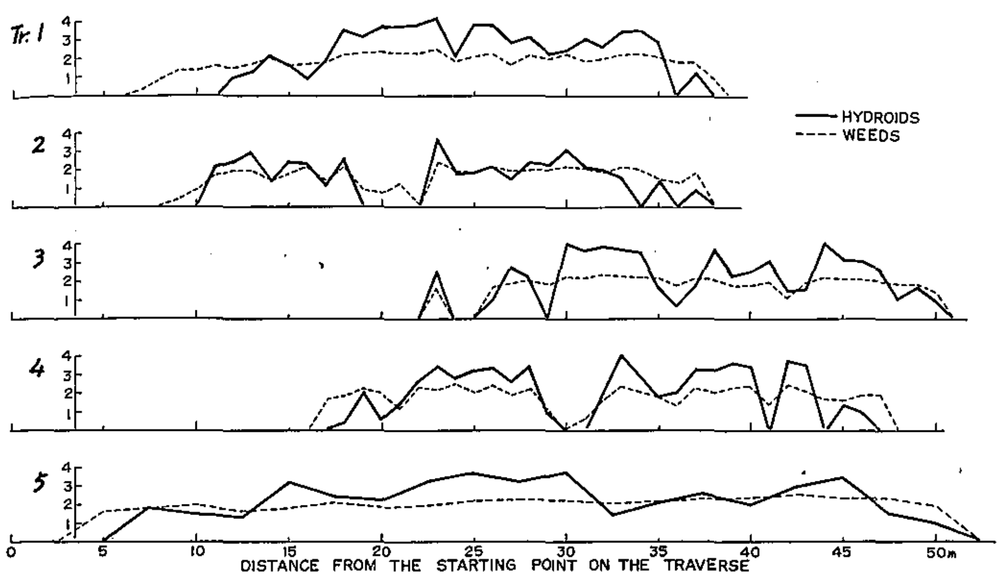

Fig. 2. The abundance of weeds (g) and epiphytic Hydrozoa (mm) on each traverse is presented in logarithm.

to analyze the relationship between Hydrozoa and algae on the species-to-species level.

II. DISTRIBUTION OF HYDROZOA AND WEEDS ON EACH TRAVERSE

To present the relationship between Hydrozoa and weeds, the crude results are shown with a profile of the traverse separately in Figs. 4–1 to 4–5. Plant symbols are shown in Fig. 3.

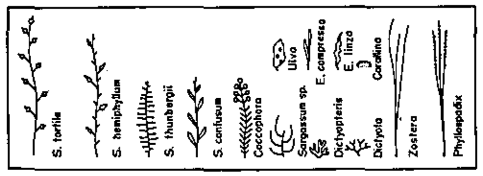

Fig. 3. Weed symbols.

Traverse 1 (Fig. 4–1). Twenty-seven algal and eight hydrozoan species were found. The dominant Hydrozoa are *Sertularella miurensis* (M), *Orthopyxis platycarpa* (0) and *Sertularella* sp. (S), each of which has a different center of distribution, and the less frequent species show patched distributions, whereas the dominant ones show a wide range of distribution. It is interesting that where a large population of *S. miurensis* exists there is no *Sertularella* sp. and less *Orthopyxis* around the point 20, the position where *Sertularella* sp. is abundant supports few other Hydrozoa. The algal distribution is complicated because various species appeared. Around the point 10 there developed *Enteromorpha* followed by *Ulva*. It is assumed that the existence of *Enteromorpha* is not important to that of Hydrozoa, namely this alga may be unfavourable as the substratum for the Hydrozoa.

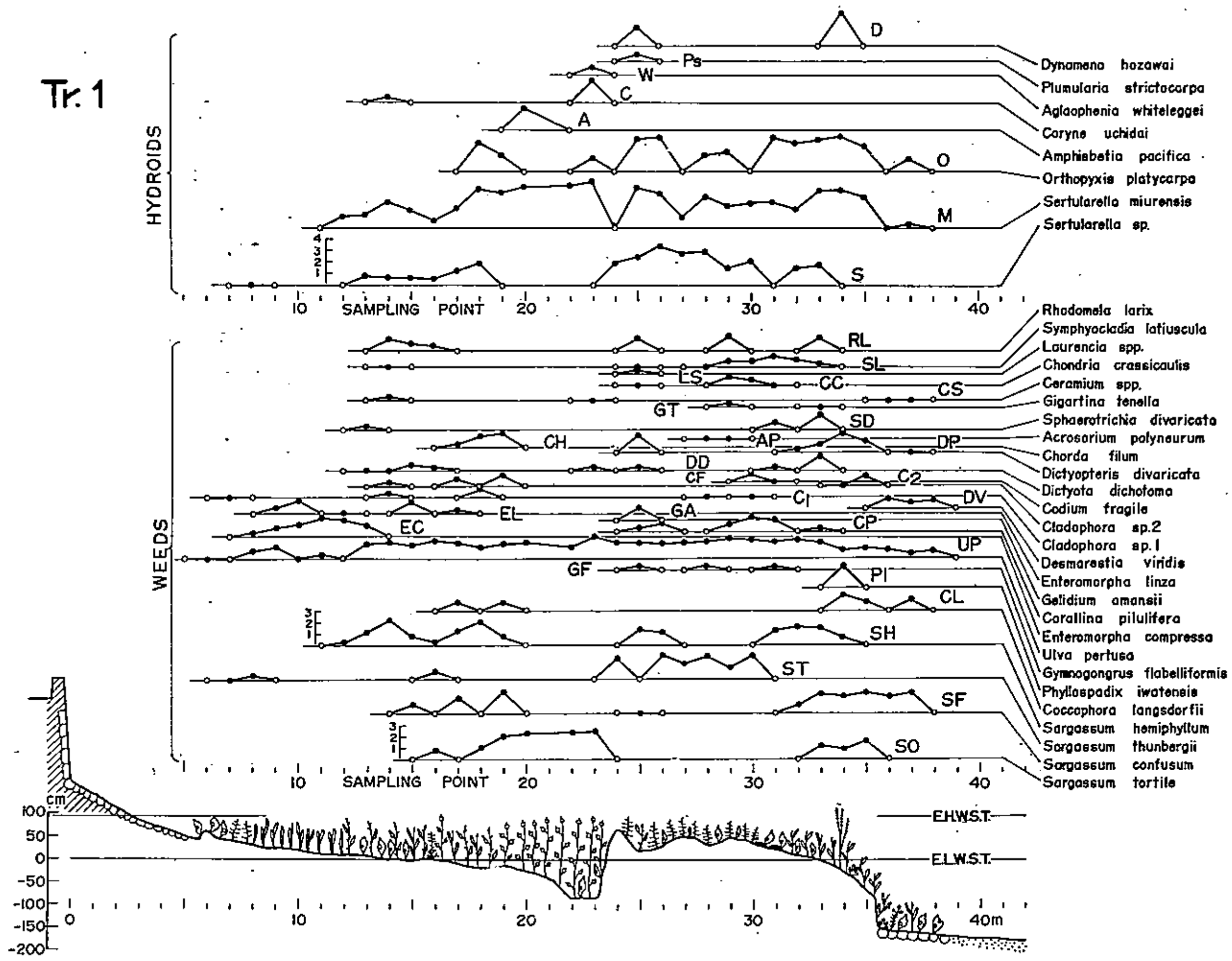

Fig. 4–1. The distribution of weeds and epiphytic Hydrozoa on Traverse 1. Ordinate: the logarithms of the amount of weeds (g) and Hydrozoa (mm) per 1/16 square meter. Open circles represent the estimation of zero. Abscissa: sampling points on the traverse. Ordinate in profile: depth in centimeters.

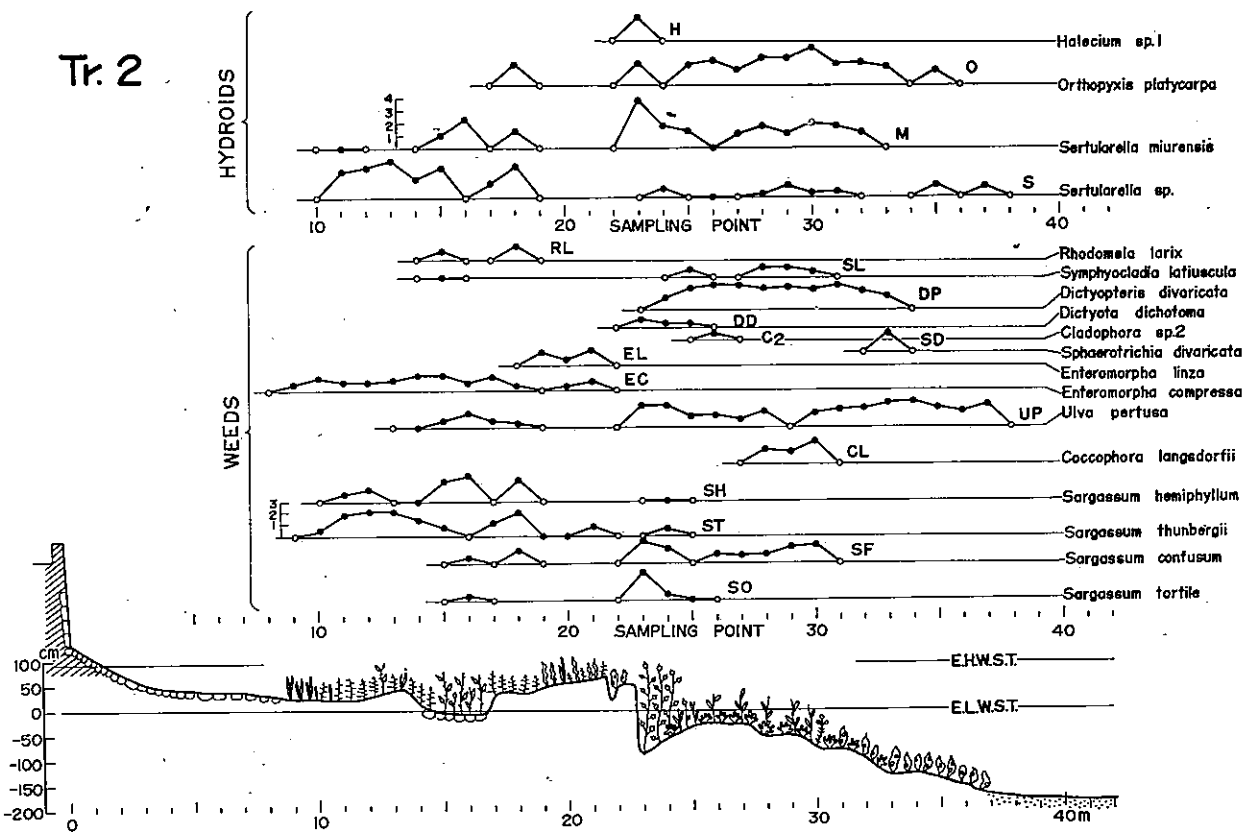

Fig. 4–2. The distribution of weeds and epiphytic Hydrozoa on Traverse 2.

Each weed has a multifarious pattern of distribution, from the wide distribution range of *Ulva* to the definite distribution of *Phyllospadix*. The main algae are those of Sargassaceae, among which *S. tortile* is dominant, growing infralittorally between points 19 and 23 where a large population of *S. miurensis* appears. It seems that in distribution *Dynamena hozawai* (D) corresponds to *Phyllospadix*, the distribution of large population of *S. miurensis* is identical with that of *S. tortile*, and the distribution of *Sertularella* sp. is considerably agreeable with that of *S. thunbergii*. Consequently, it may be suggested that the distribution of each hydroid may be influenced by the existence of a certain agla.

Traverse 2 (Fig. 4–2). Fourteen algal and four hydrozoan species were observed. *Dictyopteris divaricata* (DP) grows abundantly between points 24 and 33, where the distribution center of *Orthopyxis* appears. The distribution center of *Sertularella* sp. again corresponds to that of *S. thunbergii*, and that of *S. miurensis* to that of *S. tortile*. It is noticeable that Hydrozoa die out in the upper midlittoral zone, around the point 20, though the algal growth still continues. From the point 37 downwards the rocky bottom is replaced by a sandy one which is free from algal growth. The general figures mentioned on Traverse 1 are applicable to the present traverse.

Traverse 3 (Fig. 4–3). Although the traverse is long, the vegetational range is not so wide; the first half is free from algae probably because of the movable nature of the bottom sediments composed of scattered broken and angular small stones. Around the point 5, many *Littorina* were observed aggregated in depressions of the rocks. To the bed rock, and a little to the broken rocks, *Chthamarus* attaches, particularly abundantly near the point 20. The projection at the point 22 is covered densely with *Chthamarus* and with a few *Septifer* and *Mytilus*.

The projected rock at the point 33 is covered by *S. tortile* in the cold seasons, but in the spring tides in April and May, this alga dies out and becomes detached, and *Enteromorpha* appears to occupy the empty sites. From the points 38 to 45 there are abundant *Mytilus*, especially on the seaward side of the rock.

Twenty-six algal and eight hydrozoan species were recorded. There again *S. miurensis* and *Orthopyxis* show a wide range of distribution starting with the appearance of algae and ending with the disappearance of them. *Ulva*, as on the previous two traverses, is distributed almost uniformly throughout the vegetated area. It may be recognized from the graph that the general figures of the relation between dominant Hydrozoa and algae mentioned before are also seen in the present case. *Amphisbetia pacifica* (A) appears in some quantity, the distribution of which seems to correspond to that of *Coccophora*. The distribution center of *Orthopyxis* seems to correspond to those of *S. hemiphyllum*, *Coccophora* and *S. confusum*.

As shown in Traverse 1, the submerged situation in low water, between points

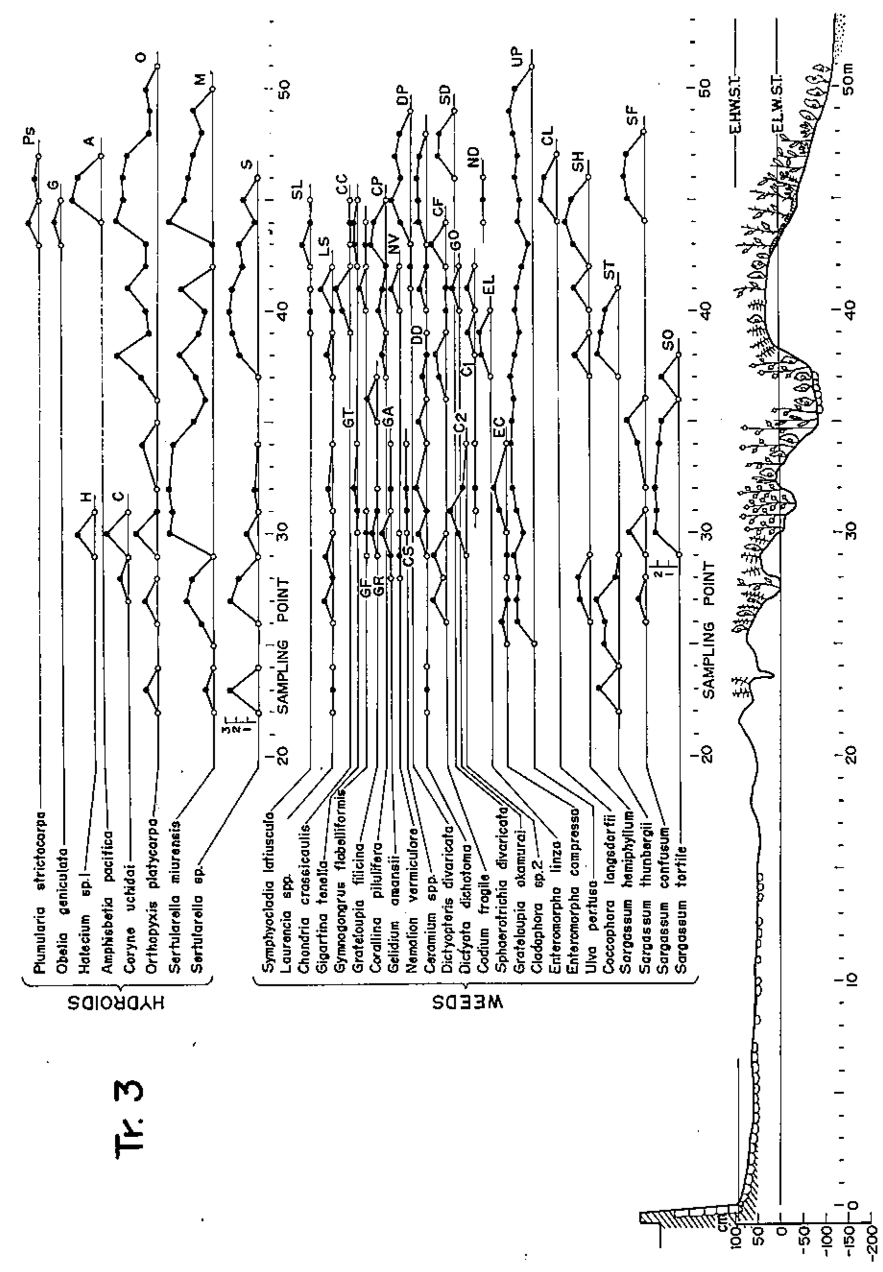

Fig. 4–3. The distribution of weeds and epiphytic Hydrozoa on Traverse 3.

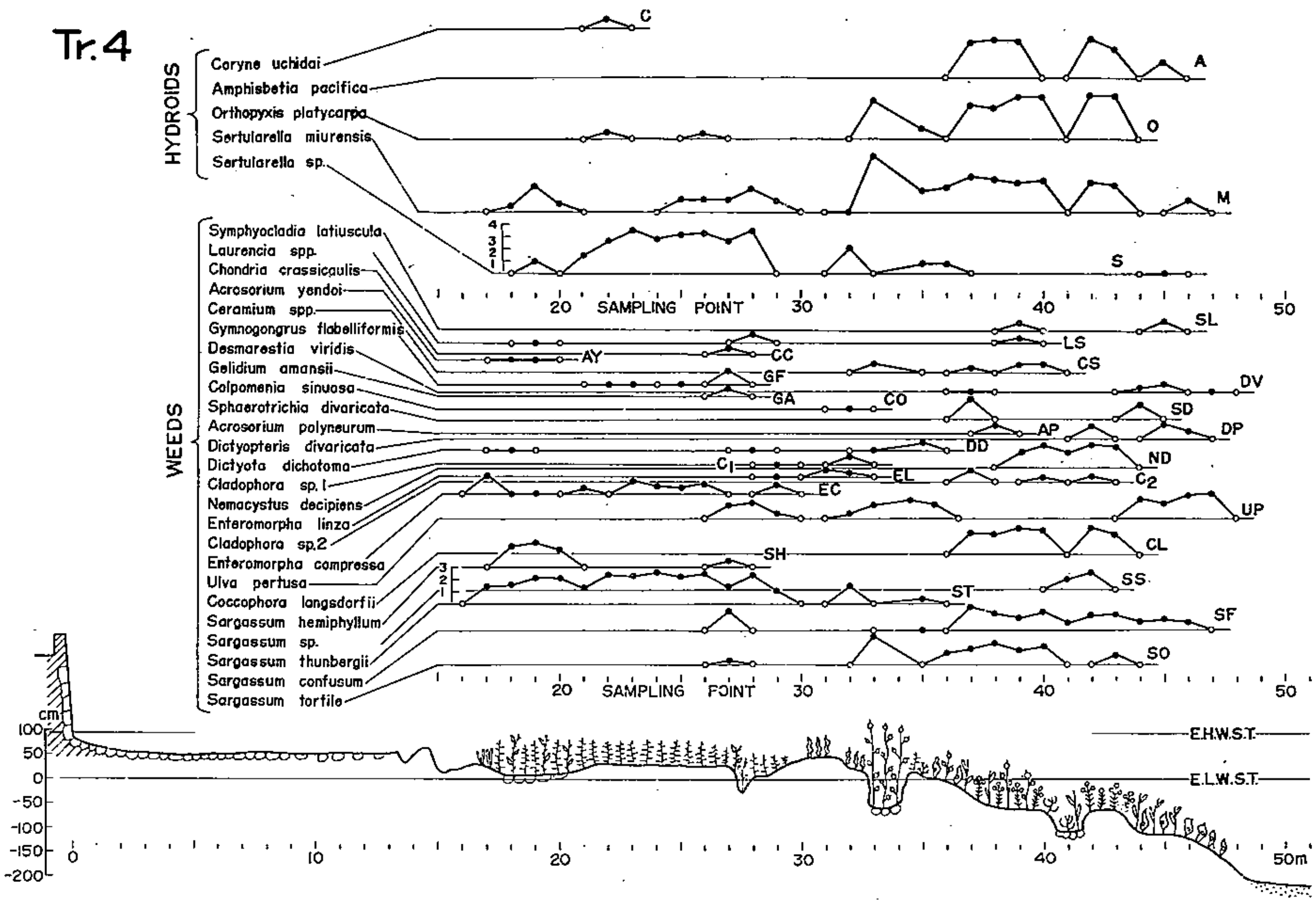

Fig. 4-4. The distribution of weeds and epiphytic Hydrozoa on Traverse 4.

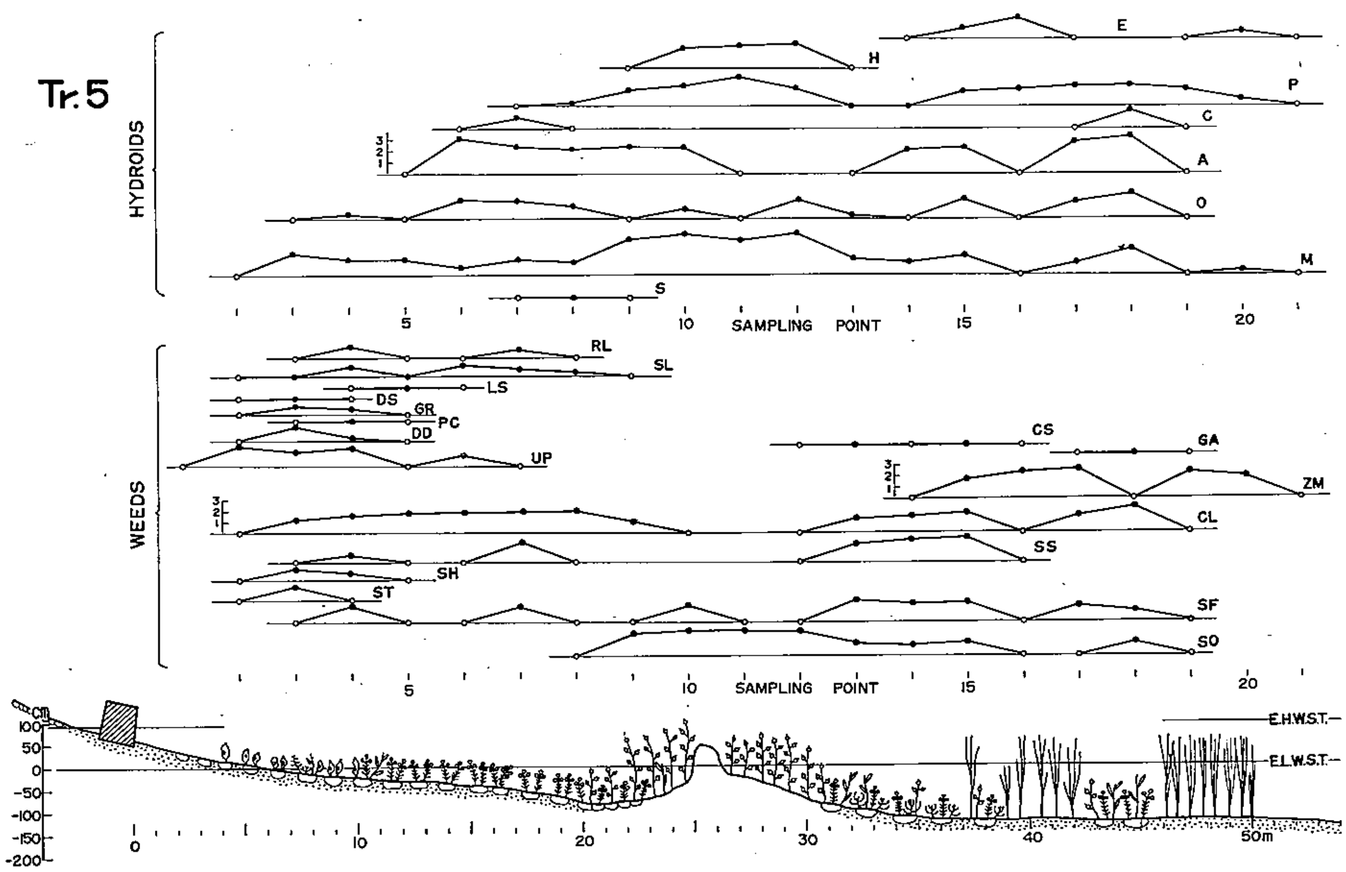

Fig. 4-5. The distribution of weeds and epiphytic Hydrozoa on Traverse 5.

30 and 38 where the *S. tortile* forest appears, supports the large population of *S. miurensis*, and at the same time, *Sertularella* sp. dies out there. An adverse relationship is obvious on the *Mytilus* bed where *S. thunbergii* and *Sertularella* sp. flourish and a decrease of *S. miurensis* and *Orthopyxis* occurs.

Traverse 4 (Fig. 4–4). As mentioned in the section of the method, the present traverse was set on the typical vegetation of *S. thunbergii* ranging from the point 17 to around the point 30 where a dense carpet of this alga developed. On the corner of the traverse (Fig. 1) the projected rock is covered densely by *Chthamarus*. On a first third of the traverse animals similar as on Traverse 3 appear.

Twenty-five species of algae and five of Hydrozoa appeared. The *S. thunbergii* bed is almost pure with a few epiphytic *Enteromorpha*. It is shown that the distribution of *Sertularella* sp. seems to correspond to that of *S. thunbergii* and the distribution center of the most frequent species, *S. miurensis*, is identical with that of *S. tortile*. Though it was presumed that the distribution of *Orthopyxis* corresponds to that of *S. hemiphyllum* on Traverse 3, the present results do not indicate such a figure. This Hydrozoa is distributed in a way similar to *Coccophora*.

Traverse 5 (Fig. 4–5). Seventeen algae and eight Hydrozoa were observed. On the middle of the traverse there is a projecting rock exposed to air at low tide, the rocky part supports *S. tortile* and is also a suitable habitat to a thecate hydroid, *Aglaophenia whiteleggei* (W), just below the extreme low water spring tide (E.L.W.S.T.) line.

It is interesting to note that *S. thunbergii* is almost absent from the traverse, probably because of the nature of the bottom and submerged situation, and the fact is well correlated with the absence of *Sertularella* sp. Further, there is a well developed *Coccophora* region on the stones and boulders in the sand throughout the traverse, which fact seems to be correlated with the distribution of *Amphisbetia*. Another remarkable feature of the traverse is the presence of *Pycnotheca mirabilis* (P) and *Clytia edwardsi* (E), the range of the latter seems to be correlated with the distribution of the new component of vegetation, *Zostera*.

The briefly described pictures on each traverse give the general figures of the distribution of Hydrozoa and algae. The distribution of epiphytic Hydrozoa on the shore seems to be influenced by the distribution of particular algae, and Hydrozoa may not simply be indifferent in respect of their algal substrata as shown previously (Nishihira, 1965). These relations are to be analyzed further in the following sections.

III. ZONATION OF HYDROZOA AND WEEDS

1. General tendency of algal preference of Hydrozoa

The amount of the colonies of Hydrozoa in millimeter per 100 g of each of the major groups of algae, Chlorophyta, Phaeophyta, Rhodophyta and submerged

Table 1

Table 1. The average mass of hydrozoan colonies (mm) per 100g. weeds of four major groups. Ch: Chlorophyta, Ph: Phaeophyta, Rh: Rhodophyta, Z: Zosteraceae, t: total weeds.

		Coryne	*Halecium*	*Orthopyxis*	*Clytia*	*Obelia*	*Dynamena*	*S. miurensis*	*Sertularella* sp.	*Amphisbetia*	*Pycnotheca*	*Plumularia*	*Aglaophenia*	TOTAL
Tr. 1	Ch			3.25				9.43	0.22					12.90
	Ph	4.25		207.02				1703.93	221.28	5.20			0.17	2141.85
	Rh			370.22			23.60	328.09	161.80					883.71
	Z						793.10							793.10
	t	2.83		157.78			21.14	1154.40	153.19	0.58			0.12	1490.04
Tr. 2	Ch			18.17				5.41	2.70					26.28
	Ph		4.85	95.34				375.20	117.59					592.98
	Rh													
	t		3.37	71.52				262.44	82.54					419.87
Tr. 3	Ch			6.81				6.30	3.11			0.22		16.44
	Ph	5.15	1.92	693.92				2091.00	68.32	30.56		2.25		2893.12
	Rh			25.66		2.63		19.74	267.76			3.95		319.74
	t	2.81	1.05	382.83		0.14		1144.91	52.32	16.68		0.34		1601.08
Tr. 4	Ch							2.38	2.85					5.23
	Ph			408.92				406.53	273.79	117.92				1207.16
	Rh	8.77		5.26					35.09					49.12
	t	0.13		360.11				358.19	241.86	103.82				1064.11
Tr. 5	Ch													
	Ph	2.73	11.46	21.12				654.16	0.05	277.65	28.90			996.07
	Rh									119.29				119.29
	Z				9.32			1.84			14.24			25.40
	t	1.78	7.44	13.73	2.79			425.63	0.03	59.96	23.04			534.40
W	Ch			7.05				6.25	2.10			0.06		15.46
	Ph	2.14	3.15	289.58				960.20	157.03	95.37	5.49	0.02	0.04	1513.02
	Rh	1.04		145.13		0.83	8.70	127.12	148.03	14.08		2.07		44.70
	Z				8.56		64.90	1.69			13.08			88.24
	t	1.53	2.20	208.07	0.57	0.03	4.58	675.84	115.24	67.03	4.70	0.09	0.03	1079.91

plants, Zosteraceae, was computed for each traverse and for the whole area (Table 1). It can be derived from the table that Hydrozoa are abundant in association with, in the order of Phaeophyta, Rhodophyta, and Chlorophyta. Similar pictures were presented in the previous report, and in Bryozoa by Ryland (1962) and by Rogick and Croasdale (1949).

It may be accepted that the general figures of the distribution of Hydrozoa on the shore may have relation with that of brown algae. In the previous observations Phaeophyta, of which especially Sargassaceae, was considered to offer a very preferable substrata (Nishihira, 1965). The main component of the vegetation on the rocky part of Tsuchiya coast is Sargassaceae besides a few green algae. Consequently, the detailed analysis is limited to those algae belonging to Sargassaceae and Zosteraceae in the following sections. Zosteraceae is included because it grows in particular sites of the bottom.

2. Concrete zonation on each traverse.

The concrete zonation of Hydrozoa and weeds was determined after Katô *et al.* (1952) as follows; for each traverse the percentage composition of the colony and thallus numbers in each sample was estimated and presented by the confidence intervals in 90 percent reliability. As to the number of weeds and Hydrozoa, species significantly more abundant than the expected mean values, which were calculated on the basis that all species on a traverse would occur in a uniform way irrespective of the difference in species, were used to determine the zonation, though these charts are not presented in the present paper. There are various sizes of colonies, ranging from about 1mm in length like those just after metamorphosis to the fully grown old colonies of several decimeters. Such a large colony is formed by the union of hundreds of colonies according to their growth, as commonly seen in *S. miurensis* (Nishihira, unpublished). Therefore, it is not satisfactory to determine the zonation of Hydrozoa judging only from the colony number. The zonation derived from the number analysis was slightly modified by the figures obtained from the colony mass analysis in which Hydrozoa with values larger than the expected mean were treated as the species constituting the zone. This procedure was also applied to weed zonation.

The zonation figures obtained on each traverse through such a procedure are shown together in Fig. 5, which may prove that the general aspects described in Figs. 4–1 to 4–5 are valid. Among them, the relations between *Sertularella* sp. and *S. thunbergii* on several traverses, *Amphisbetia* and *Coccophora*, *Dynamena* and *Phyllospadix* and between *Clytia* and *Zostera* are remarkable. Concerning with more frequent Hydrozoa, *S. miurensis* and *Orthopyxis*, however, not so clear relation with a single particular alga as the above was obtained.

The zone, in which *Sertularella* sp. appears for example, appears repeatedly on the traverse. The same is true in the case of other Hydrozoa and also of weeds. It is obviously an outcome of the concrete position of the points on the traverse, in

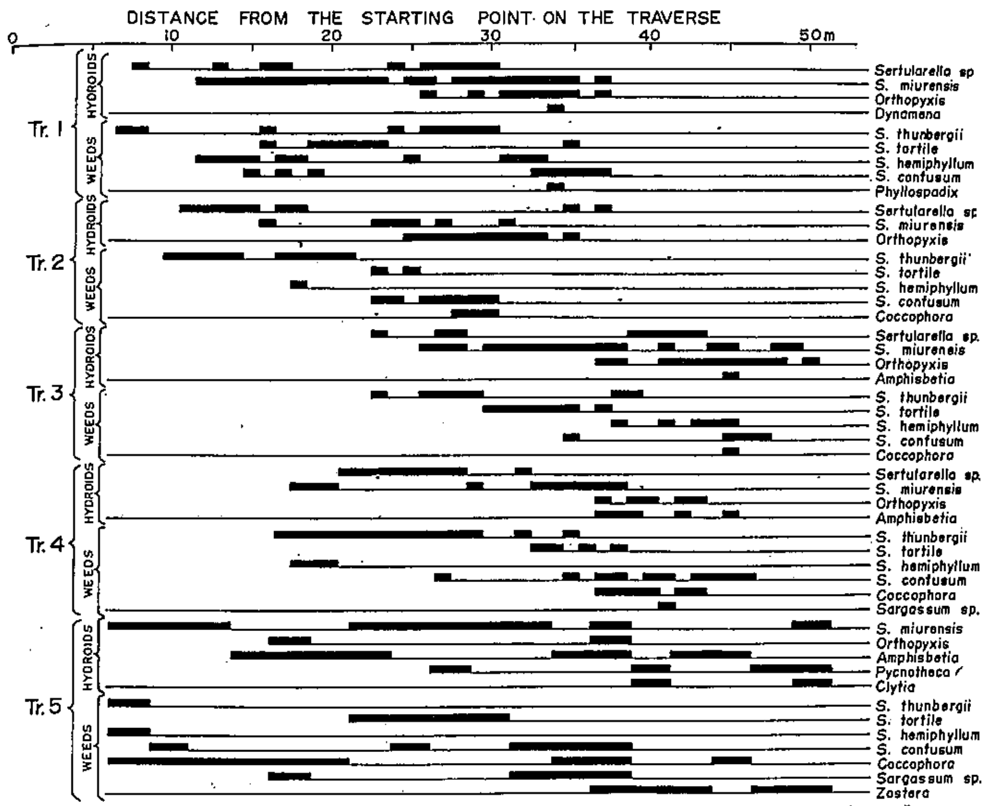

Fig. 5. The concrete zonation of weeds (Sargassaceae and Zosteraceae) and epiphytic Hydrozoa on each traverse.

other words, the parallel levels appearing repeatedly along each traverse. It is not difficult to understand such repetition in the zones in connection with the tide levels of the sampling positions.

Here, it will be noted that the zones of *S. miurensis* and *Orthopyxis* cover or extend over the various weed zones, which suggests the wide tolerance of algal preference or somewhat indifferent nature in algal selection. Two aspects may be considered as the reason of the fact that the zones of Hydrozoa are torn to pieces; one is the lack of preferable algae at the point and another is the high situation of the algal growth on the traverse. It is quite natural that the disappearance of algae is always in company with that of Hydrozoa.

3. Vertical distribution of Hydrozoa and weeds

Because the tidal level seems to have a great influence on the distribution of hydrozoan populations, several graphs were made for each traverse for the dominant algae and Hydrozoa. An example of Traverse 4 is shown in Fig. 6.

On Traverse 1, the sampling points are scattered from the upper midlittoral

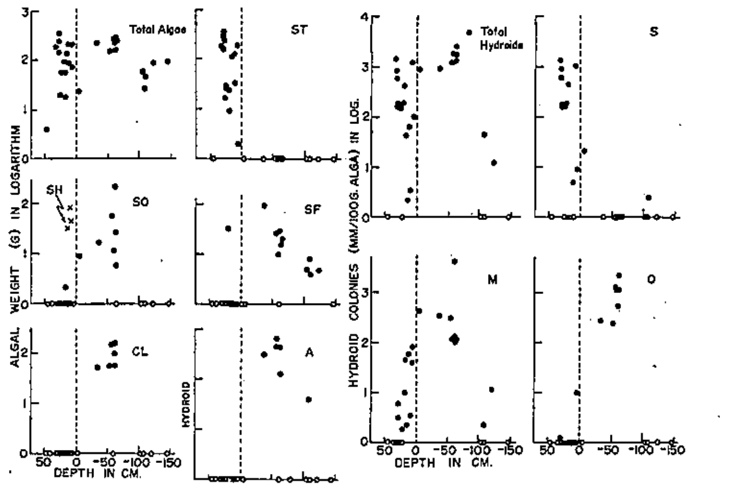

Fig. 6. The vertical distribution of weeds and epiphytic Hydrozoa on Traverse 4. Open circles represents the estimation of zero.

down to the infralittoral zone to the depth of about 160cm with the mode of occurrence around the standard line. The figures show that *S. thunbergii* is restricted to the midlittoral zone and does not penetrate into the infralittoral zone, while *S. tortile* shows quite an opposite nature of distribution. *Sargassum hemiphyllum* concentrates around the depth of zero, and *S. confusum* shows a tendency of occurrence similar to *S. tortile*. *Ulva*, as mentioned before, ranges through almost all levels. As to Hydrozoa, remarkable figures are presented by *Sertularella* sp. which occurs abundantly above the standard line like *S. thunbergii*. *Sertularella miurensis* shows no clear figures of its vertical distribution, but it can be said that the center of its abundancy occurs in the infralittoral zone. *Orthopyxis* shows the position of its distribution center intermediate between that of *Sertularella* sp. and *S. miurensis*, namely around the standard line, the infralittoral fringe, where *S. hemiphyllum* flourishes.

On Traverse 2, no particular description is necessary except for the lower occurrence of *Orthopyxis*, which shows the distribution similar to that of *Dictyopteris divaricata* (DP).

One Traverse 3, there is a similar tendency of the distribution as on Traverse 1. Here, *Amphisbetia* appears infralittorally in the same way as *Coccophora*.

On Traverse 4, it is quite interesting that the distribution of *Orthopyxis* shows a different trend in comparison with that of *S. hemiphyllum*. It suggests the importance of the properties of the growing position of weeds other than tidal level. As obvious on the profile of the traverse (Fig. 4–4, Fig. 5), *S. hemiphyllum* grows on the landward depressed portion with isolated water at low tide around the point 20. On Traverse 1 (Fig. 4–1), the importance of the growing position of

weeds may be demonstrated more obviously. On that traverse, *S. hemiphyllum* grows rather abundantly at two positions, one around point 15 where it is protected from the open water by the rocks, and another between the points 30 and 35, where the wave agitation seems to be stronger. The distribution center of *Orthopyxis* is in the *S. hemiphyllum* zone which is rather exposed to the wave action. *Amphisbetia* seems to distribute in accordance with *Coccophora* also on Traverse 4.

Almost all weeds develop under the standard line on Traverse 5, the fact is attributed to the particular nature of the bottom sediments of the traverse. *Clytia* seems to be restricted to the deeper position where the *Zostera* belt appears.

4. Vertical zonation

The zonation determined based on mere dominancy at a given sampling point has inevitably some unreasonableness. For example, in Fig. 4–4, the sample from the deepest part at the point 46 shows a high percentage value (100%) of *S. miurensis* and the vertical zone of the species was decided to extend to that depth. It is, however, quite obvious that at the point 46, the colony size (and also colony number) is very small (or few) in comparison with that at the other points. If a single species occurred in a given sampling point, the point is determined as the zone of the species even when the biomass is very scanty. Further, on the contrary, even when a relatively large population occurs in a point other than in the one decided as the zone of the species as mentioned above, the zone may not be recognized because the species concerned may appear together with many other species. In order to get a reasonable figure for the vertical zonation of each species, the zone must be drawn from the abundancy of the species concerned. The dominancy relationship among Hydrozoa in a given sample cannot be got through such method, this aspect of the population will be gained from the results presented before.

In Fig. 7, the vertical zonation determined from the quantity analysis is

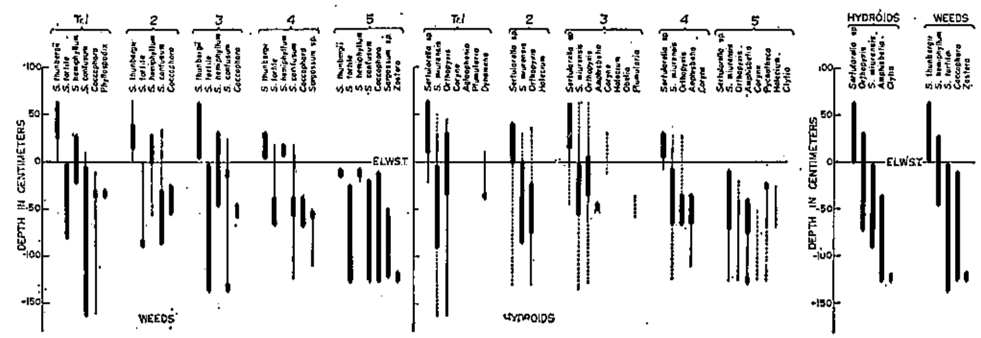

Fig. 7. The vertical zonation of weeds (Sargassaceae and Zosteraceae) and epiphytic Hydrozoa on each traverse and over the whole area.

presented. The standard line clearly cuts the lower limit of *S. thunbergii* and the upper of *S. tortile*, whereas *S. hemiphyllum* streches over the line from the lower midlittoral to the infralittoral zone. The luxuriant growth of *S. confusum* does not penetrate into the midlittoral zone like *Coccophora*. *Zostera* grows at a definite depth. There are a number of contributions on the zonation of algae on rocky coasts (Taniguchi, 1963; etc.). The environmental factors influencing the algal zonation have been discussed by many authors. The main factors are the tidal level, wave action, bottom nature, illumination and others. But the ecological factors as such are not analyzed in the present paper because it is unnecessary if the actual conditions of the algal growth on the coast are taken accurately.

In Hydrozoa the generalized figure presents the characters of their vertical distribution, namely *Sertularella* sp. in the midlittoral zone and the infralittoral fringe, *S. miurensis* in the infralittoral zone, *Orthopyxis* from lower midlittoral down to the infralittoral zone, and *Amphisbetia* and *Clytia* in the infralittoral zone.

There is a clear correlation between the vertical zones of both, viz., *Sertularella* sp. and *S. thunbergii*, *Orthopyxis* and *S. hemiphyllum*, *S. miurensis* and *S. tortile*, *Amphisbetia* and *Coccophora*, and *Clytia* and *Zostera* (Fig. 7). These correlations do not necessarily show the direct association between them. Therefore, the association between each hydroid and its aglal substratum should be analyzed.

IV. ALGAL PREFERENCE OF HYDROZOA

The preference for algal substraum is measured by the mass of colony and frequency of occurrence on each weed for each hydroid. Since the number of samples of each alga is not equal, the index of association is expressed by the formula f/F, where f is the frequency of occurrence (as percentage) of each algal substratum with which a given hydroid was found, F the total of values of percentages. When the value of the index reaches the maximum (1.0), it means the highest degree of correlation, or the full association of the species with the particular alga. The smaller the value is, the less the degree of association is with that alga. The colony ratio of each hydroid is expressed as c/C, where c and C are the relative sizes of the colony per 100g alga and the total of c of the species concerned, because of the unequal space availability of each alga in each sample.

1. Algal preference (Fig. 8)

a. Preference based on frequency of occurrence (right bars)

Obelia geniculata (G), *Aglaophenia*, *Clytia* and *Halecium* sp. 1 (H), were observed in association with only one alga and generally less in frequency and had small colony mass. *Pycnotheca*, *Plumularia strictocarpa* (Ps) *Coryne uchidai* (C) and *Amphisbetia* had somewhat large frequency and were associated with several species of algae, most of which belonged to Sargassaceae besides the case of *Plumularia*. *Coryne* on *Coccophora* and *S. tortile*, and *Amphisbetia* on *Coccophora* are remarkable. *Sertularella* sp., *Orthopyxis* and *S. miurensis* appeared in

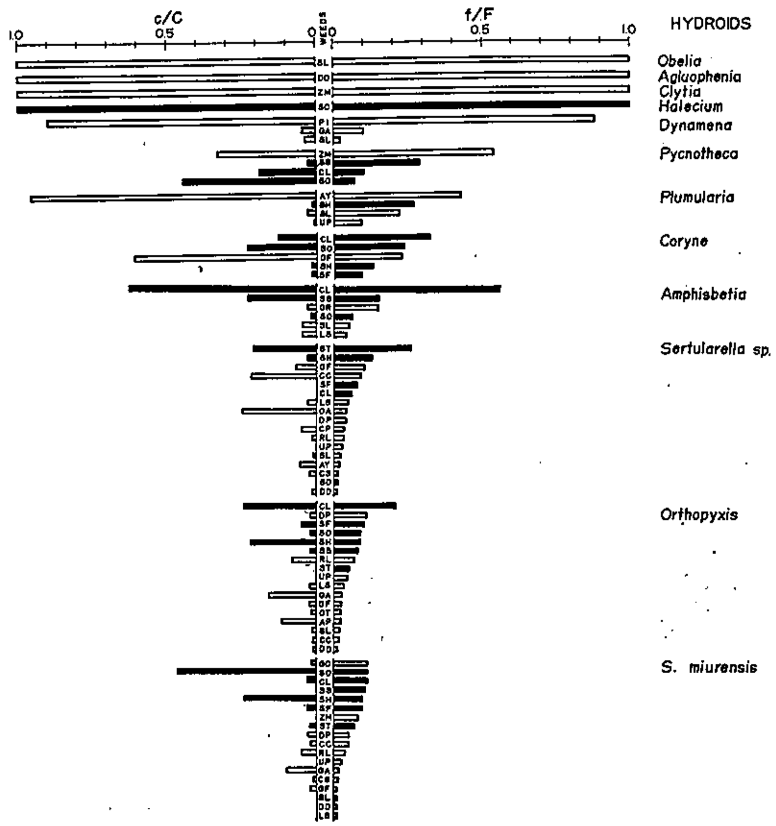

Fig. 8. The values of indices f/F and c/C in various species. Sargassaceae are designated with the solid bars. Abbreviations of weeds are as in Fig. 4. For further explanation, see text.

association with many algae but they occurred more frequently attaching to Sargassaceae than to other algae. These facts suggest that the frequent species are also intimately associated with the algae of this family. *Sertularella* sp. on *S. thunbergii* and *Orthopyxis* on *Coccophora* are striking.

b. Preference based on colony ratio (left bars)

In colony mass, the suitability of Sargassaceae is more clearly demonstrated, and further the particular association is shown markedly between *Dynamena* and *Phyllospadix*, *Pycnotheca* and *S. tortile*, *Coryne* and *S. tortile*, *Coccophora* and *Gymnogongrus*, *Sertularella* sp. and *S. thunbergii*, *Chondria* and *Gelidium*, *Orthopyxis* and *Coccophora* and *S. hemiphyllum*, and between *S. miurensis* and *S. tortile* and *S. hemiphyllum*. *Clytia* is intimately associated with *Zostera*. It is noticed that the colony is concentrated in a few particular algae even in the cases of very frequent Hydrozoa occurring on various algae. *Gymnogongrus*, *Chondria* and *Gelidium* are not abundant in the area, so that the actual role in distribution of the epiphytic Hydrozoa is not so large.

Generally the high values of f/F are in company with high values of c/C, which means that the alga used frequently by Hydrozoa supports a large population. Therefore, the role of algae which have large values of these indices is extremely important in determining the distribution of epiphytic Hydrozoa. In the cases of *Amphisbetia-Coccophora*, *S. miurensis- S. tortile* and *Sertularella* sp.–*S. thunbergii* these figures are recognized. The relation between Hydrozoa and their algal substrata can be understood more clearly and the correlation suggested in the previous sections may be proved to be true.

Here, it is concluded that most Hydrozoa are frequently observed in association with Sargassaceae, and moreover a given hydroid shows great preference for a particular algal species. Consequently the distribution of a hydroid is much affected by the distribution of its suitable alga.

2. Algae as the substratum of Hydrozoa.

Though the algal preference of Hydrozoa has been shown, there is another reciprocal analysis evaluating the alga as the substratum of Hydrozoa. The dominancy relation among Hydrozoa on each alga was calculated. The dominant species on each alga based on colony number are as follows; *Ulva-S. miurensis; Dictyopteris-Orthopyxis* and *S. miurensis; S. tortile-S. miurensis; S. confusum-S. miurensis; S. thunbergii-S. miurensis* and *Sertularella* sp.; *S. hemiphyllum-S. miurensis; Sargassum* sp. -*S. miurensis; Coccophora-S. miurensis* and *Orthopyxis; Rhodomela-S. miurensis* and *Orthopyxis;* and *Zostera-Pycnotheca.* The dominant Hydrozoa on each alga based on the frequency of occurrence are; *Ulva-S. miurensis; Dictyopteris-Orthopyxis; S. tortile-S. miurensis; S. confusum-S. miurensis; S. thunbergii-Sertularella* sp.; *S. hemiphyllum-S. miurensis; Sargassum* sp.-*S. miurensis; Coccophora-S. miurensis* and *Orthopyxis; Gymnogongrus-Sertularella* sp. The dominant Hydrozoa on each alga based on colony mass are as shown below: *Ulva-Orthopyxis* and *S. miurensis; Dictyota-Orthopyxis* and *S. miurensis; Dictyopteris-S. miurensis; S. tortile-S. miurensis; S. confusum-Orthopyxis* and *S. miurensis; S. thunbergii-Sertularella sp.; S. hemiphyllum-S. miurensis* and *Orthopyxis; Sargassum* sp.-*Amphisbetia* and *Orthopyxis; Coccophora-Orthopyxis* and *Amphisbetia; Gymnogongrus-Sertularella* sp.; *Chondria-Sertularella* sp.; *Rhodomela-Orthopyxis* and *S. miurensis; Zostera-Pycnotheca* and *Clytia.* Each figure shows similar results.

Generally the frequent and common species dominate on various algae. *Enteromorpha, Sphaerotrichia divaricata* (SD) and *Nemacystus decipiens* (ND) have no epiphytes though they are abundant in the present area. As these, the feeble, hairy and slimy algae seem to be unfavourable. On the other hand, spreading, shrub-like and hard algae are generally favourable for epiphytic animals.

Based on the percentage difference (Odum, 1950), most of the hydrozoan populations show no similarity in their compositions on any pair of the main weeds, except a few cases (Table 2). In other words, each alga has a characteristic nature as the substratum of Hydrozoa. The similar population composition on *S.*

Table 2

The Odum's percentage difference in the hydrozoan populations on the chief algae compared with each other.

	S. tortile	*S. confusum*	*S. thunbergii*	*S. hemiphyllum*	*Sargassum* sp.	*Coccophora*	*Zostera*
S. tortile	0.00						
S. confusum	85.95	0.00					
S. thunbergii	93.17	75.09	0.00				
S. hemiphyllum	**43.37**	73.33	87.38	0.00			
Sargassum sp.	93.68	69.05	93.69	92.23	0.00		
Coccophora	89.39	65.80	89.40	**49.34**	68.96	0.00	
Zostera	99.00	99.13	99.49	99.86	98.36	98.93	0.00

tortile and *S. hemiphyllum*, and *S. hemiphyllum* and *Coccophora* may be attributed to the great quantity of the dominant species, *S. miurensis* and *Orthopyxis*. *Zostera* seems to be the most particular substratum with much different population composition of Hydrozoa from others and *S. thunbergii* seems also to be the particular substratum of Hydrozoa.

V. DISTRIBUTION OF WEEDS AND HYDROZOA ON TSUCHIYA COAST

In the area studied the chief vegetations distribute in the mode briefly shown in Fig. 9. *Zostera* appears on the sandy bottom of a rather deep situation, *Coccophora*

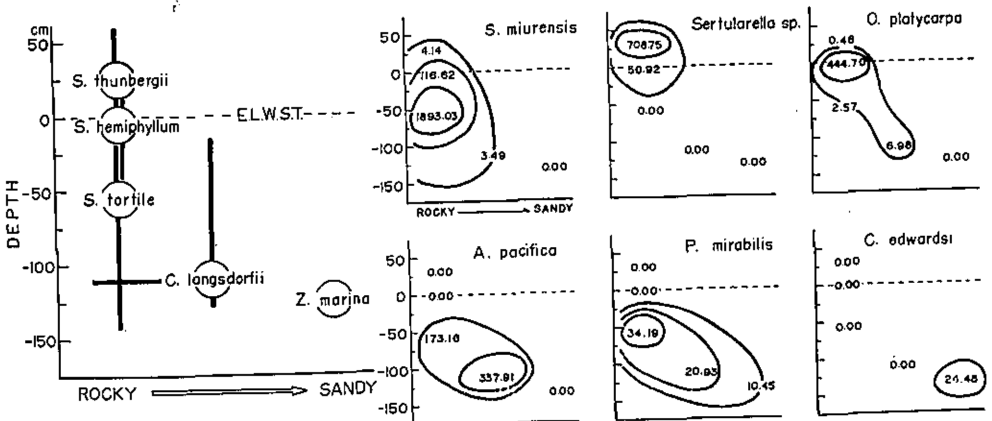

Fig. 9. The distribution of weeds and Hydrozoa on Tsuchiya coast. Left: the distribution of chief vegetations. The approximate ranges of vegetations are shown with bars and the typical positions of them by circles. Right: the distribution charts for six species of epiphytic Hydrozoa. Numerals in charts show the colony mass in mm/100g. weed. The figures indicate that the distribution center of each of six species of Hydrozoa has characteristic position along the two gradients and each species shows good accordance with its preferable alga's distribution.

is centered in the zone of stones and boulders embedded in sand and streches over a rather wide range along both gradients, though the remaining three are restricted to the rocky part, each of which has a different center of distribution along the depth gradient. There, of course, are many other remarkable vegetations such as *Enteromorpha linza* (EL) and *E. compressa* forming a distinct pattern of distribution in the midlittoral zone over the rocky bottom, though they carry no epiphytic Hydrozoa.

From the actual center of each vegetation two samples were collected and the Hydrozoa were counted. The population size of each species was written on the vegetation chart (Fig. 9) and isorithms were drawn to outline the distribution pattern. Each species has a distinct center of distribution along the depth gradient, from the shallower to the deeper level, in the order of *Sertularella* sp., *Orthopyxis*, *S. miurensis* and *Pycnotheca*, *Amphisbetia*, and *Clytia*. *Orthopyxis* has two peaks, one of which is negligible. Along the bottom nature gradient *Clytia* is restricted to sandy bottom and *Amphisbetia* to the intermediate, and the rest to the rocky bottom. Each species has a single center of distribution and in most cases these centers vary according to the species especially along the depth gradient. It seems valid that each hydroid has a characteristic center of distribution which is in accordance with that of the particular vegetation, and further most Hydrozoa taper from the center along both gradients. Thus the presumption that Hydrozoa might distribute in accordance with their favourable algal substrata on the shore may be clarified.

The question remains as to whether the high or intimate association between Hydrozoa and their particular algal substratum is a simple outcome of both forms having a similar physiology in response to the environmental factors or is caused through the mechanisms such as attractiveness of the algae for the settlement of larvae (or the positive selection of the alga by larvae). It may be suggested that the latter is the case if the various intermingling algae are sampled from the same point. Such samples appeared frequently throughout the traverse but the Hydrozoa were observed in many cases to be associated abundantly with a particular alga, from which the algal selection by larvae may be suggested. It is, of course, conceivable that the larvae settled at random on various algae but the difference in survival values of algae resulted in the particular association observed. But the observations on larval settlement of *S. miurensis* in the field suggested that it was not the case (Nishihira, unpublished).

DISCUSSION

In the present investigation, the ecological distribution of epiphytic Hydrozoa was treated with in relation to that of algae in order to check the previously suggested presumption that the epiphytic Hydrozoa have their specific algal substrata and thus distribute in good accordance with their particular algal substrata (Nishihira, 1965).

The distribution of any species is no doubt an outcome of the complicated interactions of various factors, biotic or abiotic, external or internal. The physiological characters or tolerance potency to the severe environmental factors such as desiccation or high temperature for Hydrozoa which are essentially the submerged forms are surely important. Their distribution, vertical or horizontal on the shore, would be influenced or determined in very rough scale by these factors, but the range of any species was not the main problem of the present investigation though it is not meaningless at least. Kitching (1941) wrote that "the animals of sublittoral fringe are restricted at their upper limits by exposure to air but in general range downwards extensively into the shallow sublittoral, since they are dependent on light than are the algae", and that "vertical distribution is determined chiefly by wave action in the case of one Laminaria alga, one hydroid, two polyzoans, and probably other organisms." Seasonal observations suggested that the upper limit of *S. miurensis* is probably determined by the desiccation of the growing position (Nishihira, unpublished). Within the range free from the danger of desiccation or within the tolerance range to that the hydrozoan distribution would be determined by some other mechanisms, as one of which the algal preference of Hydrozoa was suggested.

As to the snail zonation in the various marine vegetations, Bakker (1959) showed that the vertical distribution of *Littorina obtusata*, as it is found in nature, is correlated with a preference for the seaweeds on which it is found in the largest numbers. In the studies of inhabitants of submerged aquatic plants in fresh water, Krecker (1939) found that the greater the leaf dissection of a plant, the larger and usually more varied was the animal population associated with it, and Rosine (1955) suggested the "substratum preference" for a certain plant species and that the "leaf dissection, variations in periphyton and differing biochemical properties of plant species continues to increase the ecological possibilities." Harrod (1964) showed that several animals were indifferent but other animals showed preferences for a particular plant and suggested that the morphological form of a plant, the periphyton on a plant surface, the chemical nature of a plant and the habits of the various animals present may account for the considerable variation in the composition of the populations on the four aquatic plants.

Ryland (1959a and b) reported that the larvae of Bryozoa showed marked substratum preference when settling and the selection of algae accorded closely with their observed natural conditions (Ryland, 1962). And further he suggested that the selection plays an important role in determining the distribution of these species on the shore. There was a species which showed the preference for the alga which was less clearly related to the ecological distribution of the adult on the shore. He concluded that the selection of substratum by settling larvae played an important role in maintaining species at suitable tide levels.

There also are reports describing that no such correlation exists between vegetation and its inhabitant. There is a fact that "the motile fauna in the area showed no change which could be correlated specially with the change in the algal vegetation" (Kitching, 1937). Sloane *et al.* (1961) working on the fauna and flora associated with algae growing beyond the low water level of spring tides, concluded that "a clear preference for particular algae as a substrate is not shown by any species." So Ryland (1962) considered there emerged a problem that species living on the shore may show striking preferences of substratum, whereas those living in the infralittoral do not. The life form of the animals concerned would have a great meaning in the discussion of such a problem. The fact that the motile animals have the potency of locomotion while the sedentary forms have generally not from the time of their settlement on must be remembered. As shown so far, there is a remarkable association between Hydrozoa and algae even in the infralittoral zone.

Uchida et al. (1963) reported briefly on the animals living on marine algae or marine plants and recorded seven Hydrozoa from several weeds, and stated that *Tubularia radiata* is distributed in the mouth of Akkeshi Lake associating with *Zostera marina.*

On the data obtained through the traverse examination, analysis was undertaken from several aspects, algal species, vertical tide level and bottom nature, all of which were considered to have direct or indirect role on the distribution of Hydrozoa. In general the colony mass of total Hydrozoa showed good correlation with the total algal mass, the fact does not necessarily deny the algal preferential nature of Hydrozoa. The correlations are attributed to the great dominancy of Sargassaceae on the shore, for the family is very favourable for Hydrozoa. As already described, there are various algae from preferable ones to unpreferable ones. These algae such as of the Sargassaceae were very preferable and had the greatest importance in determining the hydrozoan distribution in the area studied, while the opposite, unpreferable, cases were represented mainly by Chlorophyta such as *Enteromorpha* and *Cladophora.* The vertical distribution of each hydroid was explained mostly to be correlated with that of its preferable algae.

The degree of association between Hydrozoa and algae was analyzed from three aspects, namely frequency of occurrence, colony mass and colony number, all of which presented similar figures in general. Though there are some differences between each two of them, further analysis as to the seasons of larval settlement, seasonal growth of algal thalli, growth rate of Hydrozoa, etc., will bring about improved comprehension. The growth of a colony and season of investigation may have an important influence on the results obtained. Summer when the present investigation was undertaken is the season in which *Sargassum* spp. die out and are replaced by new young plants of the same taxon. As will be reported elsewhere the newly grown young *S. tortile* carried a great number of young colonies (about 1mm in length) of *S. miurensis* in August to September, just after the present investigation was completed. The average size of this Hydrozoa was not larger than that of the others because a majority of these young colonies appeared.

In the gradient analysis the abstract distribution pattern of Hydrozoa in relation to that of algae was clearly demonstrated. Each hydroid has the distribution center in a definite position along the two gradients. The particular figure of hydrozoan distribution is not considered to be an outcome of the response of Hydrozoa directly to both gradients, but to its definite preferable alga which will be influenced far more directly by the both factors than Hydrozoa. It is considered, of course, that there would be a direct limitation of the Hydrozoa by these factors. Round *et al.* (1961) reported that a hydroid, *Sertularia operculata*, growing on a boulder, was smothered by the heavy sedimentation when transported from the rapid to the protected bay, and also Colman (1940) reported that the hydroid, *Dynamena pumila*, growing on the Laminarian holdfast was smothered by the sedimentation. Thus the direct influence of the nature of the bottom on the survival of Hydrozoa is actual. The direct limitation by the tide is more easily assumed, namely the upper limit of hydrozoan growth is directly determined by the tolerance of the species to the desiccation as suggested before. The ability of *Sertularella* sp. to inhabit the midlittoral zone may be in part attributed to the great tolerance to desiccation, but the more conceivable mechanisms of its particular distribution are probably due to its attachment position on the proximal portion of the thallus where a damp situation is maintained even when the *S. thunbergii* bed is exposed to the direct sun. The similar portion of attachment of a hydroid, *Dynamena pumila*, on a thallus of *Ascophyllum nodosum* which grows higher in the midlittoral zone was reported (Colman, 1940). Here, the distribution pattern of Hydrozoa on an algal thallus becomes important. The problem will be treated separately. The biotic factors other than algal species perhaps affect the distribution pattern of Hydrozoa, especially its microdistribution on an algal thallus as shown by Katô *et al.* (1961).

If the importance of algal selection of Hydrozoa as an important factor of its distribution on the shore are accepted, the next problem arises concerning the mechanisms of the association between alga and Hydrozoa. In general the association of both forms starts from the settling of larvae onto the algal thallus. Consequently the larval ecology is essential for the progress of the present study. And it may be valuable to compare the present results with the figures of the other coasts.

SUMMARY

The ecological distribution of the epiphytic Hydrozoa was studied on Tsuchiya coast near the Marine Biological Station of Asamushi. In total 12

Hydrozoa and 41 species of algae and marine plants were recorded on five traverses set on various vegetations.

Sargassaceae, being dominant in the rocky area of the shore, serves as the preferable substrata for Hydrozoa, and the distributions of most Hydrozoa were affected by that of this family. Several Hydrozoa showed considerable preference for particular weeds and thus good accordance in ecological distribution with their respective preferable weed. These particular associations are; *Sertularella* sp. -*Sargassum thunbergii*, *Sertularella miurensis*-*Sargassum tortile*, *Orthopyxis platycarpa*-*Sargassum hemiphyllum* and *Coccophora langsdorfii*, *Amphisbetia pacifica*-*Coccophora*, and *Clytia edwardsi*-*Zostera marina*. The first three species of Hydrozoa were very common and could be observed on various algae though they respectively showed great preference for a particular alga.

Considerable variation in compositions of hydrozoan population on various algae existed. Each alga showed no similarity in its associated population except in a few cases. *Sargassum thunbergii* and *Zostera marina* support populations different from others.

Vertical and horizontal distribution of the main vegetations and their epiphytic Hydrozoa on the shore were shown along the depth and bottom nature gradients. Each hydroid had a different distribution center along two gradients showing good correlation with that of a particular alga.

It is suggested that the algal selection by the settling larvae has great importance in establishing a particular association and consequently in determining the distribution of the species on the shore.

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