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journal or publication title	The bulletin of the Marine Biological Station of Asamushi, Tohoku University
volume	12
number	2-3
page range	75-92
year	1965-03-28
URL	http://hdl.handle.net/10097/00131286

BULLETIN OF THE MARINE BIOLOGICAL STATION OF ASAMUSHI,
VOL. XII, NOS. 2 and 3, 1965

THE ASSOCIATION BETWEEN HYDROZOA AND THEIR ATTACHMENT SUBSTRATA WITH SPECIAL REFERENCE TO ALGAL SUBSTRATA[1)]

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The relation between sedentary organisms and attachment substratum is of ecological interest. There have accumulated a number of evidences that the larvae of marine invertebrates search for a suitable substratum on or in which they occur, and many invertebrate larvae have an ability to delay metamorphosis until they find a suitable substratum (cf. Williams, 1964). Detailed studies of the association between Bryozoa and their algal substrata were made by Rogick and Croasdale (1949) in the region of Woods Hole and by Ryland (1962) in British waters. Other works are fragmental descriptions scattered throughout taxonomic papers. The association between Bryozoa and algal substrata is in part explained by the particular selectivity of the larvae (Ryland, 1959a, b).

As to Hydrozoa, there is no extensive work on the association with algal substrata in our country, although occasional descriptions are found in faunal and taxonomic papers (Yamada, 1950a, b, 1959, etc.). Uchida *et al.* (1963) described briefly the fauna inhabiting marine algae and marine plants in their report on the fauna of the Akkeshi region, Hokkaido. Katô *et al.* (1961) discussed the distribution pattern of the hydrozoan colonies attached on Sargasso-algae and suggested the important role of the interspecific interaction between the Hydrozoa in determining their micro-distributions. They have also been studying in the laboratory on the mechanisms of the mentioned interaction (Katô *et al.* 1962, 1963, 1964).

The observations reported in this paper were made mainly during the summers of 1962 and 1963 along the coast of Asamushi and its vicinity in Aomori Prefecture, northern Honshû, Japan.

Here I express my cordial thanks to Prof. Mutsuo Katô, of the Biological Institute of the Tôhoku University, for his kind direction during the present work and for his critical reading of the manuscript. Thanks are also due to Prof. Eturô Hirai, Director of the Marine Biological Station of Asamushi, and to the staff members of the Station for their helpful criticisms. The Hydrozoa were

1) Contributions from the Marine Biological Station of Asamushi, Aomori Ken, No. 323.

identified by Prof. Mayumi Yamada of the Hokkaido University, and the algae by Prof. Masahiko Takamatsu of the Hirosaki University, both to whom I extend my gratitude. The snails collected by the bait method were sent to Dr. Tadashige Habe, National Science Museum, Tôkyo, for identification, and my thanks are due to him.

METHODS

At the time of each collection of the Hydrozoa, the associated substrata were recorded. Frequent visits were made to a number of shores which have various kinds of bottom and various degrees of exposure to wave action, to collect the Hydrozoa. Each collection was made from the midlittoral zone down to the shallow infralittoral zone, about four meters deep. Besides the shore collection, diving was also done to collect various kinds of Hydrozoa.

Some Hydrozoa have been known to occur on a variety of shells and ascidians. In order to collect these animals other methods were employed. The snails, by the bait method, were collected from the various vegetation types along the coast of Tsuchiya. Fish meat was set as a bait in several dense algal areas and the snials on or around the bait were collected 30 minutes after the setting. One psecies of ascidian and two of snails were dredged from the bottom of about 30 m in depth off the Marine Biological Station of Asamushi.

In such a survey, a fairly large number of hydrozoan species could be collected though neither biomass nor colony number could be measured accurately. In each collection, only the occurrence of the associations between the algae and Hydrozoa was recorded, irrespective of biomass and the number of colonies obtained.

For the nomenclature of the Hydrozoa and algae, the writer follows Yamada (1959) and Segawa (1959), respectively, and the names of all algal species examined in the present study are listed in the Appendix Table.

OBSERVATIONS AND DISCUSSION

I. ASSOCIATION BETWEEN THE HYDROZOA AND ATTACHMENT SUBSTRATA

1. *General description of associations.*

Table 1 shows the association between the Hydrozoa and their attachment substrata. Below the infralittoral fringe on the rocky coast, Hydrozoa were observed attaching to rocks, stones, and boulders, which are categorized as 'stones and boulders' in the table. 'Shells and carapaces' refers to the shells of mollusks and carapaces of crabs, mostly of *Pugettia quadridens* which inhabits the seaweeds. Only one colony of *Plumularia strictocarpa* and one of *Orthopyxis platycarpa* were collected from the carapace of the carbs. 'Wooden structures' refers to the bottom of a boat or submerged wooden structures such as piles and submerged boats.

Table 1. The occurrence of Hydrozoa on various types of substratum.

	HYDROZOAN SPECIES (Abbreviation)		Substrata								
			Stones and boulders	Shells and carapaces	Wooden structures	Annelid tubes	Bryozoans	Hydroids	Ascidian tests	Algae	Total number of observations
ATHECATA	*Coryne uchidai* Stechow	(C)	3							28	31
	Hydrocoryne miurensis Stechow	(Hm)	20		12						32
	Tubularia simplex Alder	(Ts)		3					8		11
	Hydractinia epiconcha Stechow	(He)		13							13
	Cytaeis japonica Uchida	(Cj)		18							18
	Bougainvillia sp.	(B)								8	8
	Proboscidactyla flavicirrata Brandt	(Pf)				19					19
THECATA	*Halecium* sp. 1	(H)								9	9
	Halecium sp. 2	(H_2)	4	15							19
	Halecium sp. 3	(H_3)								2	2
	Campanularia sp.	(Cs)								4	4
	Orthopyxis platycarpa Bale	(O)	3	5	4		3			252	267
	Clytia delicatula (Thornely)	(Cd)							3	8	11
	Clytia edwardsi (Nutting)	(E)								25	25
	Obelia geniculata (Linné)	(G)		1	2		4			54	61
	Obelia dichotoma (Linné)	(Od)	5		7					2	14
	Hebella sp.	(Hs)						9			9
	Lafoea fruticosa (M. Sars)	(L)		1					12		13
	Dynamena hozawai (Stechow)	(D)								3	3
	Sertularella miurensis Stechow	(M)	1		1				1	300	303
	Sertularella spirifera Stechow	(Ss)							3		3
	Sertularella sp.	(S)		5					1	129	135
	Amphisbetia pacifica Stechow	(A)		1						47	48
	Pycnotheca mirabilis (Allman)	(P)								15	15
	Antenella secundaria (Gmelin)	(As)	42	16			2		6	19	85
	Plumularia strictocarpa Stechow	(Ps)	25	6	7	2			5	23	68
	Aglaophenia whiteleggei Bale	(W)	29	8						1	38
	Total number of observations		132	92	33	21	9	9	39	929	1264
	No. hydrozoan species associated		9	12	6	2	3	1	8	18	

'Annelid tubes' are those of *Potamilla myriops*, and 'Bryozoans' include two species of Bryozoa, namely, *Watersipora culculata* and *Amathia distans*, the latter is common as an epiphyte on the alga, *Sargassum tortile*. 'Ascidian tests' are those of *Chelyosoma siboja* and *Styela clava*.

Among those Hydrozoa which were found commonly on rocks and stones, several species, e.g., *Antenella secundaria*, *Plumularia strictocarpa* and *Aglaophenia whiteleggei* frequently occurred on shells, while some other Hydrozoa such as *Hydrocoryne miurensis*, etc. did not. Shells seem to be favourable substrata for many species of Hydorozoa, probably because of their wide variety of habitats.

Shells of *Chlamys farreri nipponensis* were more frequently observed to carry Hydrozoa than those of *Pecten yessoensis*. *Mytilus edulis* that grows in the infralittoral zone often carried a variety of Hydrozoa, e.g., *Obelia geniculata*, *Sertularella* sp., *Plumularia strictocarpa*, *Clytia delicatula* and *Orthopyxis platycarpa*, while another mussle, *Septifer virgatus*, had no attached Hydorozoa probably owing to its high position in the midlittoral zone.

Hydrozoa that are commonly found on rocks usually do not make a colony on algae as shown by *Hydrocoryne miurensis* and *Aglaophenia whiteleggei*, and most algal associations found in *Antenella secundaria* and in *Plumularia strictocarpa* were indirect ones as will be shown in some detail later.

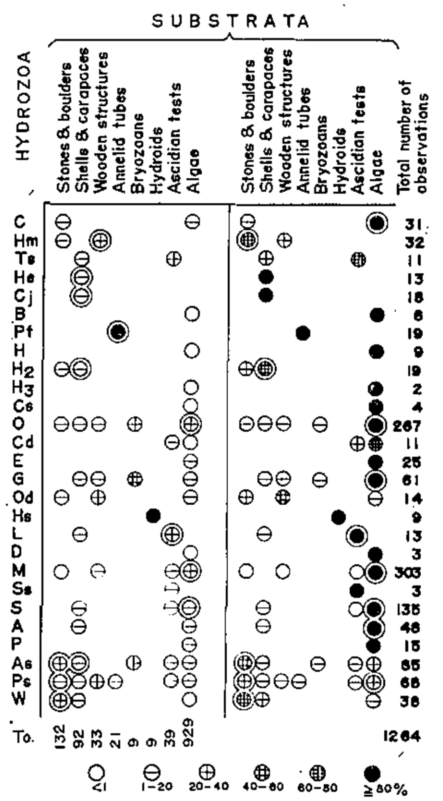

Fig. 1. The association of the common Hydrozoa with various types of substratum. Values significantly larger than the theoretical means are indicated with double cricles (for explanation see text). Left column; Occurrence of Hydrozoa on a given substratum (vertically arranged). Right column; Occurrence of a given hydroid on various types of substratum (horizontally arranged).

Table 1 is schematically presented in Fig. 1. On the left side of the figure, the hydrozoan species are arranged vertically and the dominant species on a given substratum are shown, on the right half the occurrence of hydrozoans arranged horizontally shows the suitable attachment substrata of each hydroid. Double circles indicate the dominant species on each substratum on the left side and the preferable substrata of a given hydroid on the right one. They were determined by the occurrence probability method (Katô *et al.* 1952). The percentage of the number of observations of each constituent hydroid to the total number of observations in each substratum was calculated, and those Hydrozoa which have the significantly larger percentage values than the theoretical mean (which is calculated on the basis of the same probability of occurrence in each species, namely when five hydrozoan species were found on a given substratum, the theoretical mean or percentage of each species was calculated to be 20 percent) in 90 percent reliability were considered to be the dominant species on the substratum concerned. For the right half, the same procedure was employed.

From Table 1 and Fig. 1, the following is to be noted: Hydrozoa can be grouped, in relation to algal substrata, into three groups; first, Hydrozoa which did not select an algal substratum, second, Hydrozoa which occurred on both algal and other substrata, and third, Hydrozoa which occurred only on an algal substratum. This is summarized in Table 2.

Table 2

Grouping of Hydrozoa according to the attachment substrata.

Group	Substrata		Hydroids	No. of algal spp. associated
I	Non-algae	Stones and boulders	*Hydrocoryne miurensis*	
		Shells	*Hydractinia epiconcha*	
			Cytaeis japonica	
			Halecium sp. 2	
		Annelid tubes	*Proboscidactyla flavicirrata*	
		Hydroids	*Hebella* sp.	
		Ascidian tests	*Lafoea fruticosa*	
II	Algae and others	Almost on algae	*Orthopyxis platycarpa*	32
			Sertularella miurensis	21
			Sertularella sp.	19
			Obelia geniculata	18
			Amphisbetia pacifica	15
			Coryne uchidai	7
		Equally on the both	*Plumularia strictocarpa*	15
		Seldom on algae	*Antenella secundaria*	12
			Aglaophenia whiteleggei	1
III	Algae only	Sargasso algae	*Pycnotheca mirabilis*	4
			Halecium sp. 1	3
			Bougainvillia sp.	1

2. Group I: *Hydrozoa which did not select an algal substratum.*

All the specimens of *Lafoea fruticosa* were collected from the ascidian, *Chelyosoma siboja*, except one colony which is from the snail, *Fusinus perplex*. All of these animals were dredged from the bottom of about 30 m in depth off Asamushi.

Hebella sp. is divided into two forms; the smaller form attaching to the hydroid, *Antenella secundaria* that was found on an ascidian, *Styela clava*, and another larger form attaching on the hydroid, *Aglaophenia whiteleggei*. So far, *Hebella* was observed in association only with these Hydrozoa.

A commensal hydroid, *Proboscidactyla flavicirrata*, prefers attaching to tubes of the sedentary polychaete, *Potamilla myriops*. This association is also reported from Hokkaido (Uchida and Okuda, 1941, Yamda, 1950 a, Uchida *et al.* 1963). This hydrozoan species does not make colonies on all tubes of *Potamilla*. In general, the larger tubes were more occasionally observed to be colonized than the smaller ones along the coast of Tsuchiya, though it was reported that this hydroid is found on comparatively young tubes of the same annelid in the Akkeshi region, Hokkadio (Uchida and Okuda, 1941, Yamada, 1950a). On the Californian coast *Proboscidactyla* sp. has been found in association only with *Pseudopotamilla ocellata* (Hand and Hendrickson, 1950). Hirai (1960) reported from his laboratory experiments that *Proboscidactyla* sp. could grow to form a colony on the tube margin only when a living *Potamilla* existed in the tube, and further, when the annelid was removed from its tube the hydroid degenerated to a stolon and never regenerated again to form a luxuriant colony. Thus, *Proboscidactyla fravicirrata* is considered to be in full dynamic association (Whittaker, 1962) with its substratum, *Potamilla myriops*. As to other commensal Hydrozoa, Kakinuma (1964) reported *Eugymnanthea cirrhifera* on the soft part of *Mytilus edulis* from Hachinohe, and Yamada (1950b) recorded *Ostreohydra japonica* attaching to the gill surface of *Ostrea gigas* from Hiroshima. These Hydrozoa may be in full association with their respective host mollusk.

Halecium sp. 2 was collected in the infralittoral zone on the shells of *Chlamys farreri nipponensis* from the rocky coast of Gome-jima islet off the Station.

Hydractinia epiconcha and *Cytaeis japonica* were found associating with only snails. The results of the bait method collection are summarized in Table 3, which presents obviously that each hydroid selects a particular species of snail as the substratum. Their preferences did not overlap, namely, *Hydractinia epiconcha* attached only to the snail, *Reticunassa acutidentata*, whereas *Cytaeis japonica* to only *Niotha livescens*. All of the snails carrying colonies of these

Table 3

Snail catch with fish meat bait in various vegetations. All algal vegetations are along the rocky shore at Tsuchiya and the *Zostera* belts in the sandy bottom at Ôura and Tsuchiya. Vegetations are arranged according to their vertical distribution levels. Numbers in parentheses represent the snails colonized by *Hydractinia epiconcha* and by *Cytaeis japonica* (underlined).

Snails	Vegetations					
	Sargassum thunbergii	*Sargassum tortile*	*Coccophora langsdorfii*	*Zostera marina*		
				Ôura	Tsuchiya 1	Tsuchiya 2
Thais clavigera	1					
Reticunassa fratercula	236	103	1			
Barleeia augusta	1	9				
Temanella turrita	1	21		2		
Cantharidus jessoensis		1		1		
Mitrella tenuis	3	163	42		2	9
Reticunassa acutidentata		14		266 (176)	11 (11)	8 (8)
Niotha livescens				9 (9)	15 (15)	4 (4)

Hydrozoa were collected from the *Zostera* belt and those snials, *Reticunassa acutidentata*, that inhabited rocky environment where Sargasso-algae were flourishing carried no Hydrozoa. On the rocky shore near the Shimoda Marine Biological Station, Shizuoka Prefecture, however, *Hydractinia epiconcha* was collected attaching to the snail, *Cantharus mollis*, in March. In Akkeshi Bay, *Hydractinia uchidai* is said to be the common hydroid that covers "the surface of dead shells of gastropods mainly *Neptunea arthritica* which are mostly inhabited by a hermit-crab" (Nagao, 1961). *Reticunassa fratercula*, though it is abundant and has a sculptured rugose surface, did not carry any Hydrozoa, probably because of its high position of habitat in the midlittoral zone. *Mitrella tenuis* which has a smooth shell is also free from the colonization of Hydrozoa, though it is found in the *Zostera* belt. It may be considered from the above that these two forms of Hydrozoa are principally restricted to areas of sandy bottom, selecting the snails with rugose surface as their attachment substrata. But the snail species selected may not be constant throughout the entire range of distribution of these Hydrozoa, as shown by Ryland (1962) in Bryozoa on algal thalli. Furthermore, their snail preference is considered to be stable, thus reducing competition for substratum. It is unknown whether they select a particular snail or merely survive on a particular snail after attaching to a variety of snail species. A snail carrying both species together was not observed in the present investigation at least in the case of the above two species. Sandô (1964) collected three snails of *Trittia japonica* carrying *Hydractinia epiconcha* from the *Zostera* belt at Kugurizaka near Asamushi. It selected a similar snail with rugose surface and which lives on the sandy bottom.

3. Group II. *Hydrozoa which occurred on both algae and other substrata.*

In the second group of Hydorozoa, three major subgroups can be recognized as shown in Table 2. *Aglaophenia whiteleggei* and *Antenella secundaria*, especially the former, seldom selected an algal substrata. *Antenella secundaria* selected stones and rocks far more frequently than algae, and even when it was observed on the alga the association was an indirect one, that was formed by the growth of a colony from some other substratum to the associated alga. *Plumularia strictocarpa* was found frequently on algae and on rocks but its principal substratum is considered to be other than algae.

There have been observed many Hydrozoa which are associated almost always with an algal substratum. Most of the common Hydrozoa belong to this category.

4. Group III. *Hydrozoa which occurred only on algal substrata.*

Halecium sp. 1 and *Bougainvillia* sp. were observed in association only with Sargasso-algae in the present survey, while Miss Kakinuma, of the Station, informed the writer that she found *Bougainvillia* sp. attaching to a rope hanged from a buoy in front of the Station several years ago. The distribution of *Bougainvillia* sp. was restricted to Ôura baylet near Asamushi in the present survey. *Pycnotheca* *mirabilis* attached to algae belonging to Sargassaceae, besides the several occurrences on *Zostera marina*.

Hydrozoa of the present group have a few associated algal species.

II. HYDROZOA FOUND IN ASSOCIATION WITH ALGAL SUBSTRATA

In the present section, the associations between the Hydrozoa and algae will be treated in some detail, the data of the associations are given in Table 4.

Table 4. The association of Hydrozoa with algae.

	ALGAL SPECIES	(Abbreviation)	HYDROZOAN SPECIES																		
			C	B	H	H_3	Cs	O	Cd	E	G	Od	D	M	S	A	P	As	Ps	W	TO*
CHLOROPHYTA	*Ulva pertusa*	(UP)						18			3			16	10	1		1	3		52
	Codium fragile	(CF)						2			2							2	1		7
PHAEOPHYTA	*Dictyota dichotoma*	(DD)	1					1			10			2	1			3	2		20
	Dictyopteris divaricata	(DF)						21			5			15	6					1	48
	Padina crassa	(PC)									1										1
	Chorda filum	(CH)						3		1	1			1				1			7
	Laminaria japonica	(LJ)									1										1
	Undaria pinnatifida	(UN)						3							1				1		5
	Sargassum horneri	(SR)												2							2
	Sargassum tortile	(SO)	7		7		2	23						65	1	3	4	1	2		115
	Sargassum fulvellum	(SF)	5					29			3			45	9						91
	Sargassum thunbergii	(ST)	3		1			12	1		2			32	51			1	1		104
	Sargassum hemiphyllum	(SH)	9	8	1	2	1	36	3	1	5	2		46	15			1	2		132
	Sargassum micracanthum	(SM)												3							3
	Sargassum sp.	(SS)						2						6		1	3				12
	Coccophora langsdorfii	(CL)	2					22						35	4	25	4				92
RHODOPHYTA	*Nemalion vermiculare*	(NV)						1													1
	Gelidium amansii	(GA)						11			2		1	1	4	6		2	1		28
	Corallina pilulifera	(CP)													5			2	1		8
	Halymenia acuminata	(HA)						2								1					3
	Grateloupia filicina	(GR)														1					1
	Grateloupia okamurai	(GO)						1						1							2
	Grapopeltis affinis	(GP)						1													1
	Gracilaria textorii	(GC)						2								1					3
	Gymnogongrus flabelliformis	(GF)	1					7						1	5						14
	Gigartina tenella	(GT)						4								1			1		6
	Chondrus ocellatus f. *typicus*	(CT)						5			4				2	1					12
	Chondrus ocellatus f. *crispus*	(CO)						2			1					1					4
	Chondrus armatus	(CA)						1													1
	Ceramium spp.	(CS)						2						3	1						6
	Campylaephora hypnaeoides	(CM)						3			2										5
	Acrosorium polyneurum	(AP)						1													1
	Acrosorium yendoi	(AY)													3			1	1		5
	Polysiphonia spp.	(PS)						2													2
	Chondria crassicaulis	(CC)						9			5			10	5	1		3	2		35
	Laurencia spp.	(LS)						3						1	3	1		1	3		12
	Symphyocladia latiuscula	(SL)						10			1		1	2	2	2			1		19
	Rhodomela larix	(RL)						11	2		3			9	1	1					27
ZOSTERACEAE	*Phyllospadix iwatensis*	(PI)											1								1
	Zostera marina	(ZM)					1	2	2	23	3			4			4		1		40
	* Total number of observations		28	8	9	2	4	252	8	25	54	2	3	300	129	47	15	19	23	1	929

Two hydroids, *Sertularella miurensis* and *Orthopyxis platycarpa* are dominant throughout the various algal substrata, showing a wide range of algal preference (or selection) and a great number of occurrences. *Sertularella* sp. and *Obelia geniculata* are referred to the exclusive species with a relatively small number of algal species but with a number of occurrences. It is interesting that no Hydrozoa show wide algal preference and few occurrences. If Hydrozoa do not show algal preference for the particular algal species, the total number of observations will be proportional to or correlated with the number of algal species utilized as the substratum. Table 4 seems to give such a relation at least superficially.

Here, it becomes necessary to analyze whether the Hydrozoa show a particular aglal preference or an indifferent nature in the algal selection.

1. *Algal preference of Hydrozoa.*

It is obvious from Table 5 that Phaeophyta or brown algae which include Sargassaceae are utilized as the most suitable substrata by almost all of the hydrozoan species, the next preferable ones are Rhodophyta or red algae, and the ones least preferable as algal substrata are Chlorophyta or green algae.

Table 5
Number of associated algal species in major groups with each hydroid.

	CHLORO-PHYTA	PHAEO-PHYTA	RHODO-PHYTA	ZOSTE-RACEAE	Total No. of algal spp. associated
Spp. associated/ examined	2/11	14/27	22/37	2/2	
% algal spp. associated	18.2	51.9	59.5	100	
No. of hydrozoan species	7	17	10	9	
Coryne uchidai		6	1		7
Bougainvillia sp.		1			1
Halecium sp. 1		3			3
Halecium sp. 3		1			1
Campanularia sp.		2		1	3
Orthopyxis platycarpa	2	10	19	1	32
Clytia delicatula		2	1	1	4
Clytia edwardsi		1		1	2
Obelia geniculata	2	8	7	1	18
Obelia dichotoma		1			1
Dynamena hozawai			2	1	3
Sertularella miurensis	1	11	8	1	21
Sertularella sp.	1	8	10		19
Amphisbetia pacifica	1	3	11		15
Pycnotheca mirabilis		3		1	4
Antenella secundaria	2	5	5		12
Plumularia strictocarpa	2	5	7	1	15
Aglaophenia whiteleggei		1			1
Total No. associations	11	71	71	9	162

Only a few species of green algae have been reported to support Bryozoa (Rogick and Croasdale, 1949, Ryland, 1962), and this seems to be the general characteristic of the green algae. The unfavourability of the green algae as substrata may be attributed to their life forms and to their high situation in the midlittoral zone. They are, in general, short-lived, soft and feeble like *Enteromorpha* spp. and *Monostroma* spp., filamentous like *Cladophora* spp. and having thickly haired surfaces like those of *Codium* spp. It is well known that the somewhat hard thallus of *Ulva* spp. can support the epiphytic sedentary animals such as Bryozoa, Hydrozoa, and Serpulid Polychaeta.

Among the red algae, 22 species out of the 37 exmained were found to carry ten species of Hydrozoa. The large number of associated algal species in the group of red algae is the result of a variety of species of this group, but the number of hydrozoan species associated is less than in the group of brown algae and the total number of the associations observed are not more abundant in red than in brown algae. These figures of red algae are seen again in the Bryozoa.

It is interesting to note the leading position of brown algae in preferability; the number of hydrozoan species associated with that group is largest though they include a somewhat less number of species to support the Hydrozoa than the next preferable red algae do, and the total number of observations recorded for the brown algae is fairly large. A similar tendency of the preferability of brown algae is shown in the Bryozoa (Rogick and Croasdale, 1949). Thus, brown algae are the most suitable algal substrata, having the largest number of Hydrozoa observed on the algal substrata, namely, 17 species out of 18, and a large value in the total number of associations recorded. The fact that those Hydrozoa which occurred only on algal substrata selected only brown algae suggests the remarkable suitability of this group of algae. It may be in part due to the shrub-like life forms such as Sargassaceae, and to the hard thallus. There are, also, as in green algae, filamentous small forms and hairly ones which may be responsible for the low percentage of the algal species associated.

Fig. 2, derived from Table 4 through the same procedure as in the case of Fig. 1, shows schematically the algal species selected in various degrees by the 13 frequent species of Hydrozoa. There are various hydrozoan species, from the very exclusive species such as *Bougaivillia* sp. and *Clytia edwardsi* which are restricted to a particular algal species, to the indifferent species such as *Orthopyxis platycarpa* and *Sertularella miurensis* which select 32 and 21 algal species repsectively. Even the indifferent Hydrozoa have more preferable algal species, the fact indicates that there seem to be some kind of preferable algal substrata to any species of Hydrozoa.

Coryne uchidai was frequently observed attaching to *Sargassum hemiphyllum* which flourished in the infralittoral fringe and below, and to other members of Sargassaceae in the infralittoral zone. *Bougainvillia* sp. is restricted to *Sargassum hemiphyllum* which grew in a given area in the Ôura baylet. Although the vegetation of *Sargassum hemiphyllum* is well developed along the rocky coasts outside of Ôura, the mentioned species has not been collected there.

Most of *Halecium* sp. 1 attached to the proximal parts of *Sargassum tortile* in the infralittoral zone on the rocky coast.

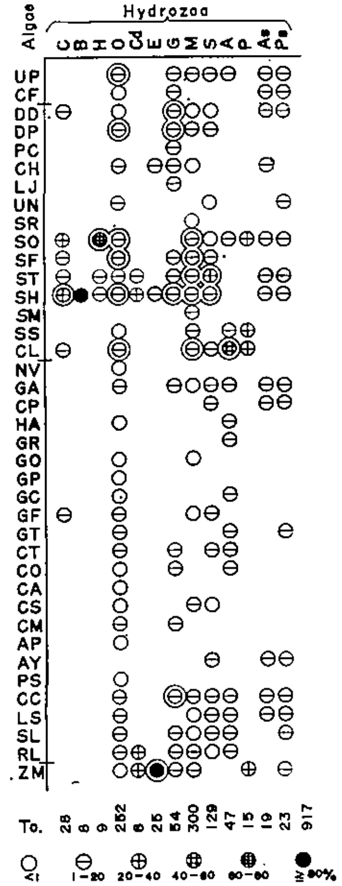

Fig. 2. The association of common Hydrozoa with various algae. The figure shows the number of occurrences of associations between various Hydrozoa and each of algal substrata (vertically arranged). Double cricles indicate the values that are significantly larger than the theoretical mean. For the details, see text.

Orthopyxis platycarpa, attaching to a variety of algae, shows preference to *Sargassum hemiphyllum*, *Sargassum fulvellum*, *Sargassum tortile*, *Coccophora lagnsdorfii*, *Dictyopteris divaricata* and *Ulva pertusa*, and exclusive of the last two listed species all of the algae belong to Sargassaceae.

Obelia geniculata attaches to various algae, but it shows preference to certain algal species. The remarkable suitability of *Dictyota dichotoma* to attachment is evident when we recall that *Obelia geniculata* was commonly observed in association with this alga from late summer to early autumn wherever the alga fluorished.

It is noteworthy that *Sertularella miurensis* showed the greatest preference to *Sargassum tortile*, though it was found associating with a variety of other algae, among which rather preferable algae were *Sargassum hemiphyllum*, *Sargassum fulvellum*, *Coccophora lagnsorfii* and *Sargassum thunbergii*.

Sertularella sp. prefers *Sargassum thunbergii* to other algae, while it selected *Sargassum hemiphyllum* rather frequently. *Amphisbetia pacifica* attaches to *Coccophora langsdorifii* frequently.

It is obvious from the facts mentioned above that the brown algae, especially those belonging to Sargassaceae, offer sutiable substrata for various kinds of Hydrozoa. And even in the Sargassaceae, each hydrozoan species selects particular algae as shown below.

Coryne uchidai — *Sargassum hemiphyllum*, (and *S. tortile*, *S. fulvellum*),
Halecium sp. 1 — *S. tortile*,
Orthopyxis platycarpa — *S. hemiphyllum*, *S. fulvellum*, *S. tortile*, *Coccophora landgsdorfii*, *Dictyopteris divaricata* and *Ulva pertusa*,
Obelia geniculata — *Dictyota dichtoma*, *Dictyopteris divaricata*, *S. hemiphyllum* and *Chondria crassicaulis*,
Sertularella miurensis — *S. tortile*, *S. hemiphyllum*, *S. fulvellum*, *Coccophora langsdorfii* and *S. thunbergii*,
Sertularella sp. — *S. thunbergii*, *S. hemiphyllum*,
Amphisbetia pacifica — *Coccophora langsdorfii*.
Clytia edwardsi shows great preference for *Zostera marina*.

Other hydrozoan species are not discussed in detail because of their low frequency in occurrence and low degree of preference for the algae.

2. *Characterization of algal substrata.*

There is a problem as to what kind of Hydrozoa a particular algal species supports significantly and most frequently. Concerning this question, a figure was prepared (Fig. 3), which shows the relative frequency of the Hydrozoa on a given algal species in the same way as in Fig. 1 (right half).

Ulva pertusa, a single favourable green alga, is colonized frequently by *Orthopyxis platycarpa* and *Sertularella miurensis*, whereas another green alga, *Codium fragile*, has no characteristic hydrozoan species. *Dictyota dichotoma* supports *Obelia geniculata* very frequently and *Dictyopteris divaricata* carries *Orthopyxis platycarpa* and *Sertularella miurensis*.

Undaria pinnatifida was observed to support *Orthopyxis platycarpa* which attached, in most cases, to a frill or to a holdfast of the thallus. Hydropolyps have characteristic shapes according to their attachment sites on the frill.

In order to collect the Hydrozoa, especially to obtain abundant

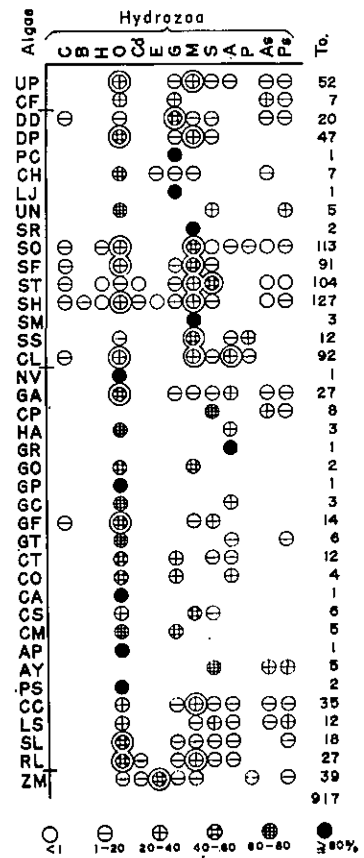

Fig. 3. The association of the common Hydrozoa with various algae. The figure shows the number of occurrences of associations between various algae and each of Hydrozoa (horizontally arranged). Presented in same symbols as Fig. 2.

Sertularella miurensis, it is advantageous to collect *Sargassum tortile*. This association is very remarkable on the rocky coasts throughout the year. This constant and continuous association presents an interesting ecological problem of great importance. *Sargassum tortile* carries, besides *Sertularella miurensis*, abundant *Orthopyxis platycarpa* on the upper part of its thallus.

Sargassum thunbergii is the most favourable substratum to *Sertularella* sp., and those algae which grow on the exposed sites on the coast often carry *Sertularella miurensis*.

Other species of Sargassaceae seem to be suitable substrata for both *Sertularella miurensis* and *Orthopyxis platycarpa*. The monthly observations show that *Sertularella* sp. survives successfully in the midlittoral zone by attaching to the proximal portion of the thallus of *Sargassum thunbergii*, whereas *Sertularella miurensis*, characteristic on *Sargassum tortile* which grows in the infralittoral zone, cannot survive successfully in the midlittoral zone. Spring tides of May, which occurs in the daytime, damage the Hydrozoa, *Sertularella miurensis*, attaching to the thallus gorwing in the infralittoral fringe. *Sertularella miurensis* prefers *Sargassum tortile* to *Sargassum thunbergii*, so it is still unknown whether *Sertularella* sp. has a wide range of tolerance to desiccation or whether it recieves an advantage by attaching to the proximal portions of *Sargassum thunbergii*, because the algae seem to serve as a cover preventing the Hydrozoa from desiccation at low tides.

Coccophora langsdorfii carries characteristically *Amphisbetia pacifica*. As other Sargassaceae, this alga offers suitable sites to *Sertularella miurensis* and *Orthopyxis platycarpa*, this is probably due to the wide torelance of these Hydrozoa in algal preference.

A red alga, *Gelidium amamsii*, is utilized for attachment frequently by *Orthopyxis platycarpa* and *Amphisbetia pacifica*, and because of the remarkable association of the latter hydroid with this alga, the Japanese name *'Tengusa-umi-kabi'* is given to *Amphisbetia paciaca*.

In general the red algae offer a less suitable substratum for Hydrozoa compared with the brown algae, whereas the shrub-like or spreading algae, e.g., *Chondria crassicaulis*, *Laurencia* spp., and *Rhodomela larix* are rather suitable. They are frequently collected and found carrying one or both of *Orthopyxis platycarpa* and *Sertularella miurensis*.

It may be noted that *Zostera marina* supports many *Clytia edwardsi*, which can be easily collected by dredging the *Zostera* plants from the deeper part of the *Zostera* belt in Ōura baylet.

It has been shown in the earlier pages of this paper that most of the hydrozoan species have a particularly preferable algal substratum and also that there really exist very preferable algal groups such as Sargassaceae. On the other hand, there also exist those algae which carry no hydrozoan epiphytes (see Appendix Table).

From the above observations some problems arise: what is the cause of the preferability and of unpreferability of the algal species as the substratum of the Hydrozoa; what are the mechanisms by which the association is induced or prevented; and is the ecological distribution of the Hydrozoa along the coast in accordance with that of their preferable algal species? It is presumable that the ecological distribution of the Hydrozoa along the coast would be influenced by that of their preferable algal species within the possible range of distribution of the Hydrozoa in relation to tidal effects. These interesting problems will be discussed at another occasion.

SUMMARY

1. Observations are presented on the associations between 27 species of Hydrozoa, of which seven belong to Athecata and 20 to Thecata, and the substrata on which they occur, with particular reference to the algae.

2. Hydrozoa are classified into three groups in relation to algal substrata, viz., Group I: Hydrozoa which do not select algal substrata, Group II: Hydrozoa which occur on both algal and other substrata, and Group III: Hydrozoa which occur only on algal substrata.

3. There are observed 18 species of Hydrozoa attaching to 38 species of algae and two of eelgrasses. Two species of green algae, 14 of brown and 22 species of red algae are recorded as the substrata of Hydrozoa.

4. The data show that many of the Hydrozoa exhibit definite preferences to substrata for attachment. Some athecate hydroids show complete exclusiveness in substratum preference.

5. Remarkable suitability of brown algae as substrata for hydrozoan attachment, especially those of Sargassaceae, are clearly shown. Furthermore, each species of Sargassaceae carries particular species of Hydrozoa.

6. Since the hydrozoan species exhibit such marked preferences for their algal substrata, it is suggested that the distribution of them along the coast may be affected by that of their preferable algal species, within the possible range of distribution of Hydrozoa in relation to tidal effects.

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APPENDIX TABLE

A list of algal species examined in the present survey with notes on associated hydrozoan species.

Key to hydrozoan species: C: *Coryne uchidai*, B: *Bougainvillia* sp., H: *Halecium* sp. 1, H_3: *Halecium* sp. 3, Cs: *Campanularia* sp., O: *Orthopyxis platycarpa*, Cd: *Clytia delicatula*, E: *Clytia edwardsi*, G: *Obelia geniculata*, Od: *Obelia dichotoma*, D: *Dynamena hozawai*, M: *Sertularella miurensis*, Ṡ: *Sertularella* sp., A: *Amphisbetia pacifica*, P: *Pycnotheca mirabilis*, As: *Antenella secundaria*, Ps: *Plumularia strictocarpa*, W: *Aglaophenia whiteleggei*.

CHLOROPHYTA

1. *Monostroma angicava* Kjellman
2. *Ulva pertusa* Kjellman (O G M S A As Ps)
3. *Enteromorpha compressa* (L.) Greville
4. *Enteromorpha linza* (L.) J. Agardh
5. *Cladophora* sp. 1
6. *Cladophora* sp. 2
7. *Cladophora wrightiana* Harvey
8. *Cladophora densa* Harvey
9. *Chaetomorpha moniligera* Kjellman
10. *Bryopsis plumosa* (Hudson) C. Agardh
11. *Codium fragile* (Suringar) Hariot (O G As Ps)

PHAEOPHYTA

12. *Ectocarpus* sp.
13. *Sphacelaria variabilis* Sauvageau
14. *Dictyota dichotoma* (Hudson) Lamouroux (C O G M S As Ps)
15. *Dictyopteris divaricata* (Okamura) Okamura (O G M S W)
16. *Padina crassa* Yamada (G)
17. *Sphaerotrichia divaricata* (Agardh) Kylin
18. *Saundersella saxicola* Okamura et Yamada
19. *Heterochordaria abietina* (Ruprecht) Setchell et Gardner
20. *Acrothrix pacifica* Okamura et Yamada
21. *Nemacystus decipiens* (Suringar) Kuckuck
22. *Desmarestia viridis* (Müller) Lamouroux
23. *Punctaria plantaginea* (Roth) Greville
24. *Punctaria* sp.
25. *Scytosiphon lomentaria* (Lyngbye) Link
26. *Colpomenia sinuosa* (Roth) Derbes et Solier
27. *Colpomenia bullosa* (Saunders) Yamada
28. *Chorda filum* (L.) Lamouroux (O E G M As)
29. *Laminaria japonica* Areschoug ? (G)
30. *Undaria pinnatifida* (Harvey) Suringar (O S Ps)
31. *Sargassum horneri* (Turner) C. Agardh (M)
32. *Sargassum tortile* C. Agardh (C H Cs O M S A P As Ps)
33. *Sargassum fulvellum* Agardh (C O G M S)
34. *Sargassum thunbergii* (Mertens) O. Kuntze (C H O Cd G M S As Ps)
35. *Sargassum hemiphyllum* C. Agardh (C B H H_3 Cs O Cd E G Od M S As Ps)
36. *Sargassum micracanthum* (Kützing) Yendo (M)
37. *Sargassum* sp. (O M A P)
38. *Coccophora langsdorfii* (Turner) Greville (C O M S A P)

RHODOPHYTA

39. *Nemalion vermiculare* Suringar (O)
40. *Gelidium* sp. (cf. *G. divaricatum* Martens)
41. *Gelidium amansii* Lamouroux (O G D M S A As Ps)
42. *Neodilsea yendoana* Tokida
43. *Corallina pilulifera* Postels et Ruprecht (S As Ps)
44. *Halymenia acuminata* (Holmes) J. Agardh (O A)
45. *Grateloupia filicina* (Wulfen) J. Agardh (A)
46. *Grateloupia ramosissima* Okamura
47. *Grateloupia okamurai* Yamada (O M)
48. *Grateloupia turuturu* Yamada
49. *Carpopeltis affinis* (Harvey) Okamura (O)
50. *Carpopeltis flabellata* (Holmes) Okamura
51. *Gloiopeltis complanata* (Harvey) Yamda
52. *Gloiopelits furcata* Postels et Ruprecht
53. *Nemastoma nakamurae* Yendo
54. *Hypnea* sp.
55. *Gracilaria textorii* Suringar (O A)
56. *Gymnogongrus flabelliformis* Harvey (C O M S)
57. *Gigartina tenella* Harvey (O A Ps)
58. *Chondrus ocellatus* f. *typicus* Okamura (O G S A)
59. *Chondrus ocellatus* f. *crispus* Okamura (O G A)
60. *Chondrus armatus* (Harvey) Okamura (O)
61. *Chrysymenia wrightii* (Harvey) Yamada
62. *Lomentaria* sp. (cf. *L. catenata* Harvey)
63. *Lomentaria hakodatensis* Yendo
64. *Champia* sp. (cf. *C. parvula* (Agardh) J. Agardh)
65. *Callithamnion callophyllidicola* Yamada ?
66. *Ceramium kondoi* Yendo emend. Nakamura }
67. *Ceramium* spp. } (O M S)
68. *Campylaephora hypnaeoides* J. Agardh (O G)
69. *Acrosorium polyneurum* Okamura (O)
70. *Acrosorium yendoi* Yamada (S As Ps)
71. *Dasya sessilis* Yamada
72. *Polysiphonia urceolata* Greville }
73. *Polysiphonia* spp. } (O)
74. *Chondria crassicaulis* Harvey (O G M S A As Ps)
75. *Laurencia obtusa* Lamouroux }
76. *Laurencia glandulifera* Kützing ? } (O M S A As Ps)
77. *Symphyocladia latiuscula* (Harvey) Yamada (O G D M S A Ps)
78. *Rhodomela larix* (Turner) C. Agardh (O Cd G M S A)

ZOSTERACEAE

79. *Phyllospadix iwatensis* Makino (D)
80. *Zostera marina* Linné (Cs O Cd E G M P Ps)