

Coarse scale distributions and community structure of hydromedusae related to water mass structures in two locations of Japanese waters in early summer

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Abstract: We observed coarse-scale (1–100 km) distributions of hydromedusae in two locations in Japanese waters, the Osaka Bay–Kii Channel area and the Tokyo Bay–Sagami Bay area in early summer. Hydromedusan assemblages, defined by cluster analysis, were divided into several groups in both areas. Distributions of the assemblages were fitted to those of water masses defined by T–S diagrams. The fitness shows that physical processes influenced the coarse-scale distributions of hydromedusae. In the semi-enclosed inlet waters (Osaka Bay and Tokyo Bay), species numbers were low. In the coastal waters (northern parts of Kii Channel and Sagami Bay), high abundance of *Muggiaea atlantica* and occurrence of specific meroplankters were recognized. Assemblages in the southern part of the Kii Channel and central Sagami Bay, which are boundary areas between both coastal and oceanic waters, showed high number of species because coastal and oceanic species occurred in these regions. Species belonging to the oceanic assemblage were distributed in southern part of Sagami Bay and were comprised of many siphonophores and some trachymedusae without meroplankters. Because the same distribution pattern of hydromedusan assemblages was recognized in both the study areas, it is considered that assemblages of hydromedusae are useful as indicators of water masses. Meroplankters, which occurred in the coastal waters (northern parts of Kii Channel and Sagami Bay), have characteristic life cycles such as asexual reproduction by immature medusae or high productivity where medusae are formed from hydroids. It is likely that such biological factors as well as physical factors influence the horizontal distribution of hydromedusae.

Key words: hydromedusae, horizontal distribution, coarse scale, physical factor, biological factor, and indicator assemblages

Introduction

Hydromedusae are ecologically important because they are typical carnivores in zooplankton communities and sometimes occur in great numbers. Many reports have shown their importance as secondary consumers in coastal ecosystems (e.g. Huntley & Hobson 1978; Larson 1987; Greeve 1994). Feeding pressures by hydromedusae affect not only zooplankton but also fish as they prey on various kinds of marine animals. Some hydromedusan species such

as *Aequorea victoria*, *Sarsia tubulosa*, *Veella lata*, and *Physalia physalis* have been reported to eat fish eggs or larvae (Purcell 1985); these species are both predators and competitors of fish larvae. As outlined above, the impact of hydromedusae on marine ecosystems is recognized to potentially be very large. To understand the ecological roles of hydromedusae in ecosystems, it is important to know their species composition and spatial distributions.

Previously, there have been several reports on hydromedusan distributions over larger scales but those over smaller scales are relatively scarce. Mega- or macro-scale (over 3000 km and 1000–3000 km respectively) distributions have been summarized by Kramp (1959, 1965, 1968) and Alvarino (1971). The relationship between mega-scale dis-

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tributions and evolution of hydromedusae has been discussed by van der Spoel (1996). Several reports on meso-scale (100–1000 km) distributions of hydromedusae have been associated with upwellings (Goy 1973) or advective processes (Gili et al. 1991; Pagès & Gili 1991; Pagès 1992). However, their meso-scale distributions in both the western Mediterranean and the southern Gulf of Mexico were influenced not by physical properties of the water but rather by the distance offshore (Gili et al. 1988; Gasca 1999). For examples of fine-scale (meters to hundreds of meters) distributions, hydromedusae have been reported to be aggregated at the convergence of Langmuir circulation cells of 100–300 m width in the Bering Sea (Hamner & Schneider 1986). Coarse-scale (1–100 km) distributions, however, have not been studied. Because the physical processes in highly productive coastal waters are not only of meso-scale but also of coarse-scale, order research on the coarse-scale distribution of hydromedusae is needed.

Together with physical factors, biological factors are important in the establishment and maintenance of plankton distribution, while affects of biological factors on the distributions of hydromedusae have not been discussed sufficiently. The Class Hydrozoa includes members with many types of life cycles; Anthomedusae, Leptomedusae, Limnomedusae, and some Narcomedusae have both periphytic asexual hydroid stages and planktonic sexual medusan stages, while Trachymedusae and another Narcomedusae have only planktonic stages. Both the asexual and sexual stages of most members of the Siphonophorae are planktonic. Although planktonic medusae are sexual stages, im-

mature medusae of some species reproduce asexually by budding or schizogenesis. Such differences in the life cycle may act as biological factors influencing the distribution of hydromedusae.

We investigated the coarse-scale distributions of hydromedusae in two locations in Japanese waters, the Osaka Bay–Kii Channel area and the Tokyo Bay–Sagami Bay area, in early summer. Environmental conditions in both sample areas were variable since they both included semi-enclosed inlets and open areas that are affected by flow of the Kuroshio Current. Osaka Bay is semi-enclosed and connected with the northern part of the Kii Channel, which lies between Kii Peninsula and Shikoku Island, about 100 km in the north–south dimension. Tokyo Bay is semi-enclosed and connected with the eastern part of Sagami Bay. Sagami Bay is located on the southeastern coast of Honshu Island, about 55 km in north–south and east–west dimensions. Osaka Bay and Tokyo Bay are among the most eutrophic waters in Japan.

The purposes of the present study were (1) to examine the distribution patterns of hydromedusan assemblages in relation to coarse-scale hydrographic features, and (2) to discuss the characters of each hydromedusan assemblage.

Materials and Methods

A sampling series was made aboard the RT/V Seiyō-Marū, Tokyo University of Fisheries from 13 to 16 June, 1997 at 13 stations along a transect from the head of Osaka Bay to the south of Kii Channel, and another series was

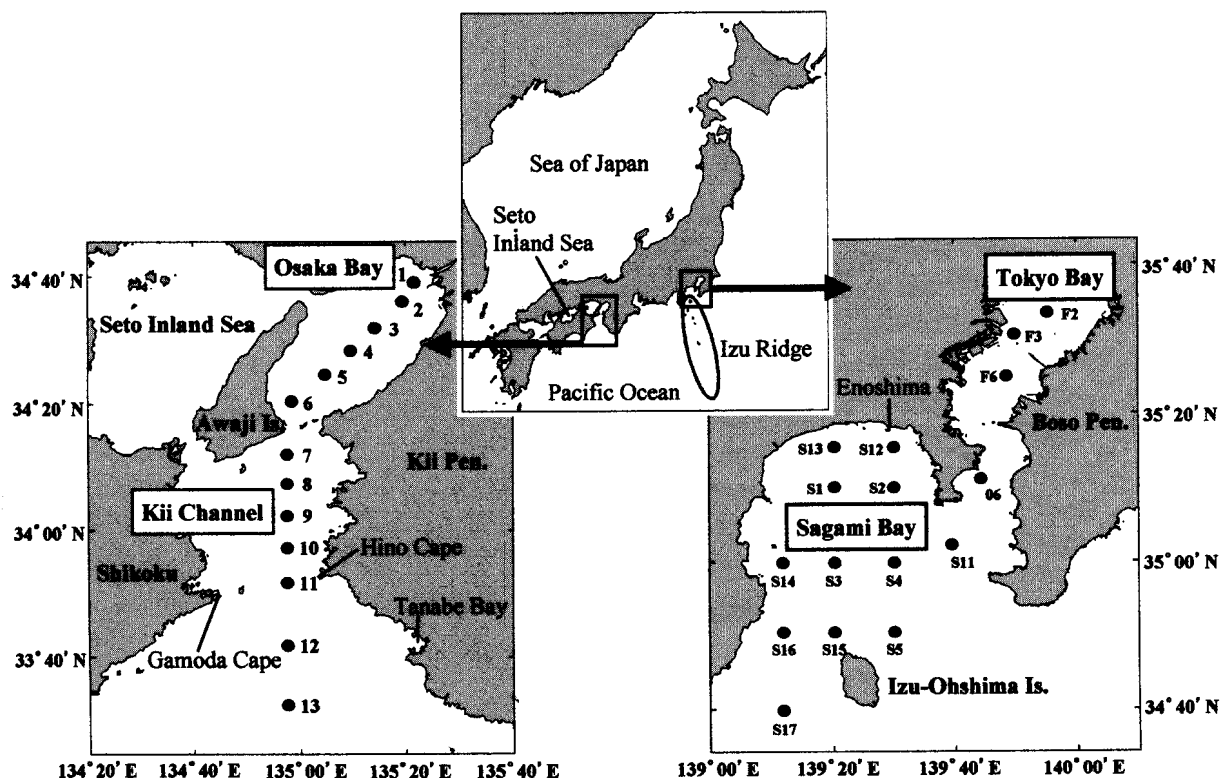


Fig. 1. Study sites: the Osaka Bay-Kii Channel area (left) and the Tokyo Bay-Sagami Bay area (right).

made from 17 to 23 June, 1998 at 16 stations in Tokyo Bay and Sagami Bay (Fig. 1).

Vertical hauls were made from 1-m above the bottom (Stns. 1–12 in Osaka Bay–Kii Channel, and Stns. F2, F3, F6, 06 in Tokyo Bay–Sagami Bay), from 50-m (Stn. S12), or from 150-m (other stations) to the surface with a NORPAC net (45-cm diameter, 0.33-mm mesh aperture; Motoda 1957) at a haul speed of 1 m/s. All samplings were carried out in the daytime. The volume of water filtered through the net was estimated using a flow-meter mounted on the mouth of each net. Samples were fixed and preserved in buffered 5% formaldehyde seawater solution immediately after sampling.

Hydromedusae were identified to species level and counted to determine the population density (number of individuals per 100 m³ of water). For three siphonophore species, *Nanomia bijuga*, *Cordagalma cordiformis*, and *Vogtia glabra*, the colony numbers could not be counted because they have many nectophores of identical shape in each colony, but only loose nectophores were identified in the net samples. Thus these three species were examined as to their presence or absence in a sample but not used in the following analysis. Numbers of colonies of the other siphonophore species were counted based on their anterior nectophores. Only the asexual polygastric stage was used in the present study.

Population density of each species was standardized prior to the analysis by calculating $\log_{10}(x+1)$. A similarity matrix between stations was constructed based on the difference in species composition using percentage similarity (Whittaker, 1952). Cluster analysis was carried out with the similarity matrix coupled with the unweighted pair-group method using arithmetic group averages (UPGMA) to classify the stations into groups.

At each station, vertical profiles of temperature and salinity were obtained using a CTD system (Neil Brown, Mark-3). T–S diagrams were plotted and used to obtain the distribution pattern of water masses.

Results

Hydrographic features

In the Osaka Bay–Kii Channel series, the T–S diagram showed the existence of three water masses (Fig. 2). The water mass from Stns. 1 to 7 was characterized by lower salinity. High salinity water was present at Stns. 12 and 13. Intermediate water existed from Stns. 8 to 11. In the present study, these water masses were named Osaka Bay Water, Southern Kii Channel Water, and Northern Kii Channel Water, respectively (Fig. 3). Bottom layers of Stn. 7 and Stns. 9–11 showed relatively higher salinity, these bottom waters were influenced by Northern Kii Channel Water and Southern Kii Channel Water, respectively.

On the other hand, four water masses were seen in the Tokyo Bay–Sagami Bay area. As shown by the T–S diagram, low salinity water was extended at Stns. F2, F3 and F6 in northern Tokyo Bay (Fig. 2). Stations located in Sagami Bay and southern Tokyo Bay were classified into three groups (Fig. 2). High salinity water was recognized at Stns. S15 and S17. Relatively lower salinity water existed at the inner stations of Sagami Bay (Stns. S1–S3, S12–S14) and Stn. 06 in Tokyo Bay. Intermediate water was existed at Stns. S4, S5, S11, and S16. We will refer to these four water masses as Tokyo Bay Water, Oceanic Water, Sagami Bay Water, and Transitional Water, respectively (Fig. 3).

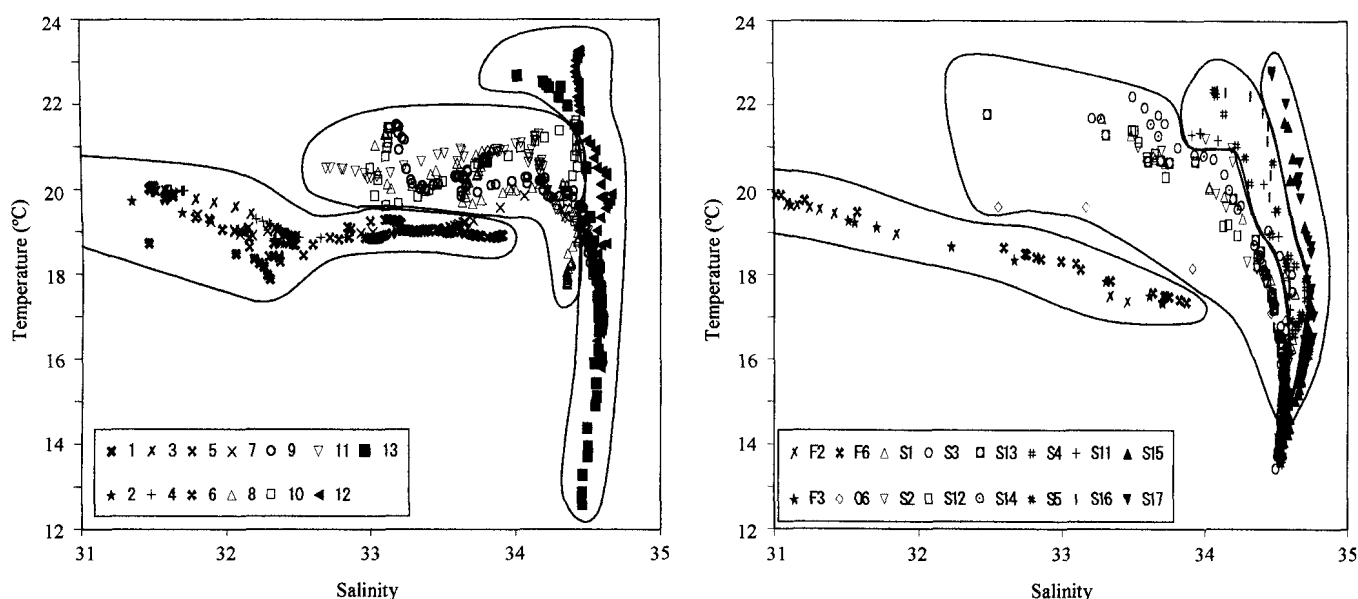


Fig. 2. T–S diagrams of the Osaka Bay–Kii Channel area (left) and the Tokyo Bay–Sagami Bay area (right). Low salinity data (below 31 PSU) in Osaka Bay and Tokyo Bay were omitted.

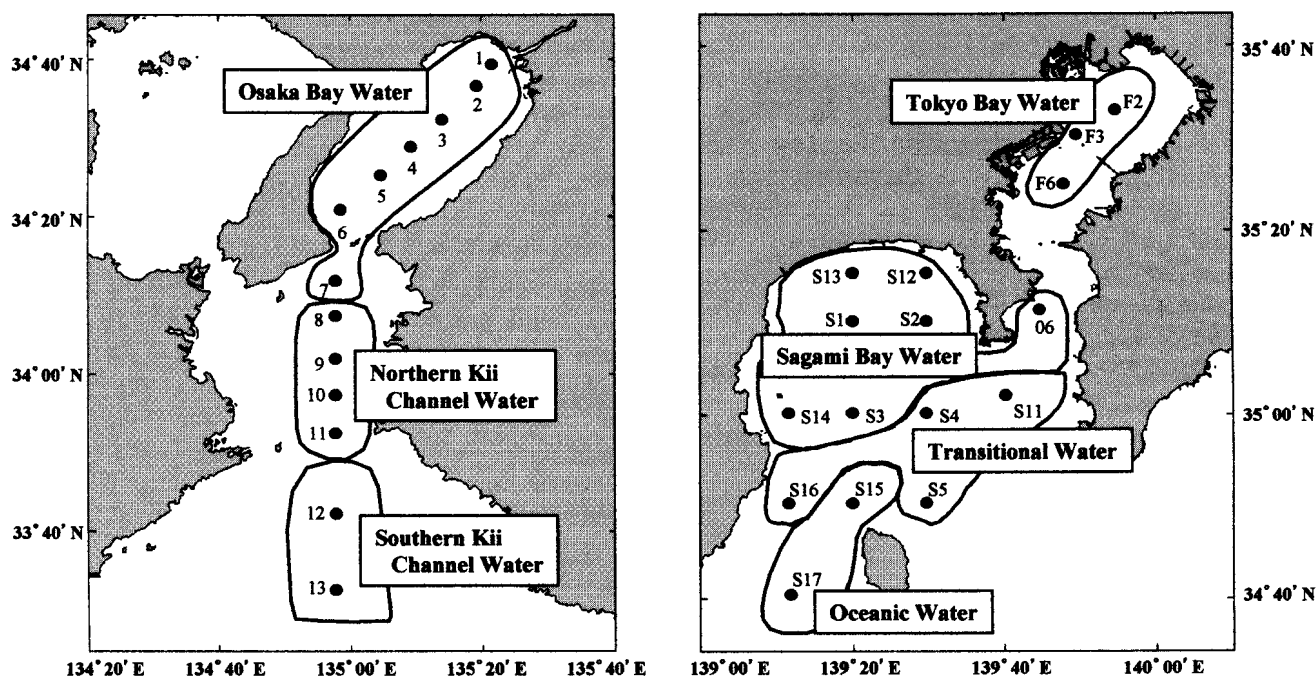


Fig. 3. Horizontal distribution of water masses defined by T-S diagrams shown in Fig. 2. The Osaka Bay-Kii Channel area (left) and the Tokyo Bay-Sagami Bay area (right).

Hydromedusae in the Osaka Bay-Kii Channel area

A total of 14 species of hydromedusae and 20 species of siphonophores were collected (Table 1). In the Osaka Bay-Kii Channel area, hydromedusae were present at all stations. The number of species per station increased from north to south. It was especially low (less than five) at stations located in Osaka Bay. At Stns. 8–11, total population densities per station were relatively high exceeding 1000 inds./100 m³.

Within the hydromedusan community in the Osaka Bay-Kii Channel area, *Muggiaea atlantica* was the most numerous species (about 40% of the total population density), being collected from all stations. *Muggiaea atlantica* occurred in abundance from Stns. 8–11 located in the Northern Kii Channel Water (over 1000 inds./100 m³, Fig. 4); highest density was at Stn. 8 (3732 inds./100 m³). *Obelia* spp. was the next most numerically dominant species (about 25% of the total population density) and was also distributed in large numbers in the Northern Kii Channel Water (Stns. 8–11, Fig. 5) with the highest density (6347 inds./100 m³) being recorded at Stn. 9. *Clytia gardineri*, *Solmundella bitentaculata*, *Aglaura hemistoma*, and *Liriope tetraphylla* were also common. Of these four species, the former two exhibited relatively high population densities at Stns. 8–11, while the latter two were numerous at Stns. 8–13. All siphonophore species, except for *M. atlantica*, occurred at low population densities.

Clustering of stations yielded two groups, Osaka Bay stations (Group 1) and Kii Channel ones (Group 2), at the 0.2 level of similarity (Fig. 6). The hydromedusan assemblage

of Group 1 was characterized by a small number of species (average 2.3) and low population densities (average 178 inds./100 m³). The most numerous species of the Group 1 was *M. atlantica*, which comprised 68% of the total number of individuals in the station group (Fig. 7). The only siphonophore collected, apart from *M. atlantica*, was at Stn. 6 *Nanomia bijuga* and occurrences of meroplanktonic hydromedusae were sporadic (Table 1). Group 2, which contained a large number of species and a high population density, could be split further into three sub station groups at the 0.65 level of similarity (Fig. 6). Subgroup 2a was composed of four stations (Stns. 8–11) located in the Northern Kii Channel Water, Subgroup 2b consisted of two stations (Stns. 12 and 13) in the Southern Kii Channel Water, and Subgroup 2c was made up of only Stn. 7 where bottom water influenced by the northern Kii Channel Water. One characteristic of the hydromedusan assemblage of Subgroup 2a was its high population density (average 6612 inds./100 m³). In Subgroup 2a, *M. atlantica* was the most numerous species, followed by *Obelia* spp. and *Clytia gardineri* (Fig. 7). The average number of species per station was 16 in Subgroup 2a. The hydromedusan assemblage of Subgroup 2b was characterized by a large number of species (average 22.5 species per station), of which *A. hemistoma* and *L. tetraphylla* dominated instead of *M. atlantica* (Fig. 7).

Hydromedusae in the Tokyo Bay-Sagami Bay area

In the Tokyo Bay-Sagami Bay area, hydromedusae appeared at all stations except Stn. F2 located in the inner-

Table 1. Population densities (individuals per 100 m³) of hydromedusae at each station in the Osaka Bay–Kii channel area. Presence of loose nectophores of the two siphonophore species, *Nanomia bijuga* and *Cordagalma cordiformis*, are shown by a plus mark. Meroplankters are shown by *, holoplankters are shown by **.

	Stations bottom depth (m) water filtered (m ³)	1 14 2.3	2 18 3.0	3 21 4.1	4 37 5.9	5 38 5.5	6 69 13.4	7 61 12.8	8 74 10.3	9 72 11.6	10 67 9.1	11 73 9.0	12 137 19.2	13 1095 23.7		
		Group 1						Group 2								
Species								Subgroup 2c	Subgroup 2a			Subgroup 2b				
Subclass Hydroidomedusae																
Order Anthomedusae*																
<i>Bougainvillia</i> sp.								8								
<i>Ectopleura dumortieri</i>		33														
<i>E. minerva</i>												5				
<i>Vannuccia forbesii</i>												4				
Order Leptomedusae*																
<i>Clytia gardineri</i>								18		321	2988	963	810	34		
<i>Clytia</i> spp.									31	49	509	219	44	13		
<i>Eucheilota paradoxa</i>		24						17		68	121	153	255	5		
<i>Obelia</i> spp.								220		78	6347	120	89	4		
<i>Sugiura chengshanense</i>									31	97		33	44			
Order Trachymedusae**																
<i>Aglaura hemistoma</i>									23	136	86	88	144	214	118	
<i>Liriope tetraphylla</i>								7	16	97	35	109	311	136	131	
<i>Persa incolorata</i>								7	16	19	26		11	21	4	
<i>Rhopalonema velatum</i>										39	9		11	16	17	
Order Narcomedusae**																
<i>Solmundella bitentaculata</i>									63	418	380	350	133	37	34	
Subclass Siphonophorae																
Order Physonectae**																
<i>Cordagalma cordiformis</i>													+	+		
<i>Nanomia bijuga</i>								+		+						
Order Calycophorae**																
<i>Abylopsis eschscholtzi</i>									10				5			
<i>A. tetragona</i>									10	17	33			52	34	
<i>Bassia bassensis</i>														21	8	
<i>Chelophyes contorta</i>														5		
<i>Diphyes bojani</i>														16	4	
<i>D. chamissonis</i>									23		17	22	33	5	8	
<i>D. dispar</i>											11	11	10	13		
<i>Eudoxoides mitra</i>												11				
<i>Lensia campanella</i>															4	
<i>L. cossack</i>											11					
<i>L. hotspur</i>											11			5		
<i>L. meteori</i>														5		
<i>L. subtilis</i>											11			5	8	
<i>L. subtiloides</i>									55	10	69	22			10	13
<i>Muggiaea atlantica</i>		85	133	24	68	294	134	681	3732	2098	2177	2553	115	97		
<i>Sphaeronectes gracilis</i>								47	10	9	22			31	8	
<i>S. irregularis</i>									10	9			11	16		
<i>Sulculeolaria chuni</i>															4	
Total population density		85	167	48	85	532	149	995	5102	12720	4354	4273	736	626		
Number of species		1	2	2	2	3	4	11	17	15	17	15	22	22		

Table 2. Population densities (individuals per 100 m³) of hydromedusae at each station in the Tokyo Bay–Sagami Bay area. Presence of loose nectophores of three siphonophore species, *Nanomia bijuga*, *Cordagalma cordiformis*, and *Vogtia glabra*, are shown by a plus mark. Meroplankters are shown by *, holoplankters are shown by **.

	Stations bottom depth (m)	F3 24	F6 27	06 307	S1 1084	S2 764	S3 1503	S12 91	S13 764	S14 414	S5 1709	S15 807	S17 545	S4 1332	S11 851	S16 816	F2 17
	water filtered (m ³)	4.0	5.9	55.6	28.4	23.5	26.8	10.5	25.9	28.1	15.2	37.7	58.5	44.5	62.7	42.0	3.2
		Group 3		Group 4													
Species		Subgroup 4a				Subgroup 4b				Subgroup 4c							
Subclass Hydroidomedusae																	
Order Anthomedusae*																	
<i>Ectopleura dumortieri</i>		100	51														
<i>Podocoryne minima</i>								10									
Order Leptomedusae*																	
<i>Clytia gardineri</i>														7			
<i>Clytia</i> spp.							7	10	4	14				16		2	
<i>Euceilota paradoxa</i>					18	4	4			4				2	2		
<i>Obelia</i> spp.		50	237	23	60	55	15	152	73	14					2	12	
Order Trachymedusae**																	
<i>Aglaurea hemistoma</i>					18	17	4	19		4	33		7	38	6	2	
<i>Liriope tetraphylla</i>					7	9	4	19	8		33	19	17	25	19	10	
<i>Persa incolorata</i>				2	11	21	15	10	8	7	13	3		2	13	2	
<i>Rhopalonema velatum</i>				2							20	8	3	2	2	2	
Order Narcomedusae**																	
<i>Solmundella bitentaculata</i>				2	7	26	11		19	7	7			29	5	5	
Subclass Siphonophorae																	
Order Physonectae**																	
<i>Cordagalma cordiformis</i>														+		+	
<i>Nanomia bijuga</i>														+			
Order Calycophorae**																	
<i>Abylopsis eschscholtzi</i>												3	5	2		2	
<i>A. tetragona</i>												5	10	2	10	7	
<i>Bassia bassensis</i>							7				13	13	3	9	2	10	
<i>Chelophyes contorta</i>							4				7	5	3	2	2	2	
<i>Diphyes bojani</i>											20		2	2	2		
<i>D. chamissonis</i>															2	2	
<i>D. dispar</i>							4					3	2	2		2	
<i>Eudoxoides mitra</i>							4				13			2	2		
<i>Lensia companella</i>														4		2	
<i>L. challengerii</i>								10									
<i>L. fowleri</i>													2				
<i>L. hotspur</i>									4								
<i>L. meteori</i>					4		4					5	2			5	
<i>L. subtilis</i>								10			20	3	7	2	2	7	
<i>L. subtiloides</i>					11	13		10	12	14				2	6	7	
<i>Muggiaea atlantica</i>			17	13	673	400	146	1448	560	317	13	3	2	202	147	71	
<i>Sphaeroneustes gracilis</i>												3	2	4			
<i>S. irregularis</i>				4	7	4	7		12	4		3					
<i>Sulculeolaria chuni</i>													3				
<i>Vogtia glabra</i>											+				+		
Total population density		150	305	45	813	549	235	1695	699	384	191	74	68	362	220	155	0
Number of species		2	3	6	10	9	14	10	9	9	12	14	14	23	17	19	0

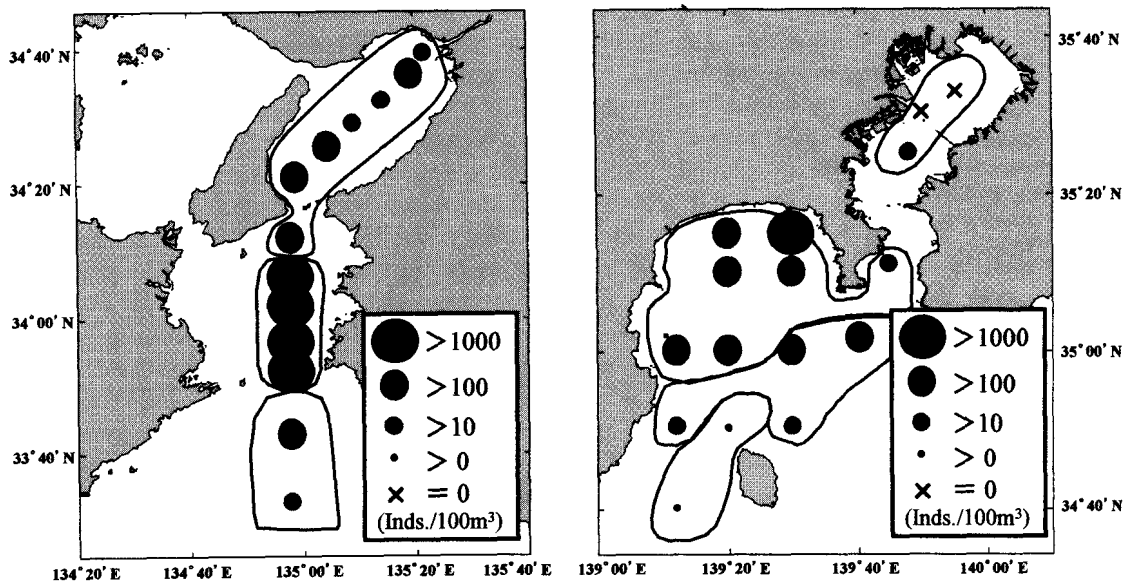


Fig. 4. Horizontal distribution of water masses and the siphonophore *Muggiaea atlantica* in the Osaka Bay-Kii Channel area (left) and the Tokyo Bay-Sagami Bay area (right). Circles show population densities of this species (individuals per 100 m³).

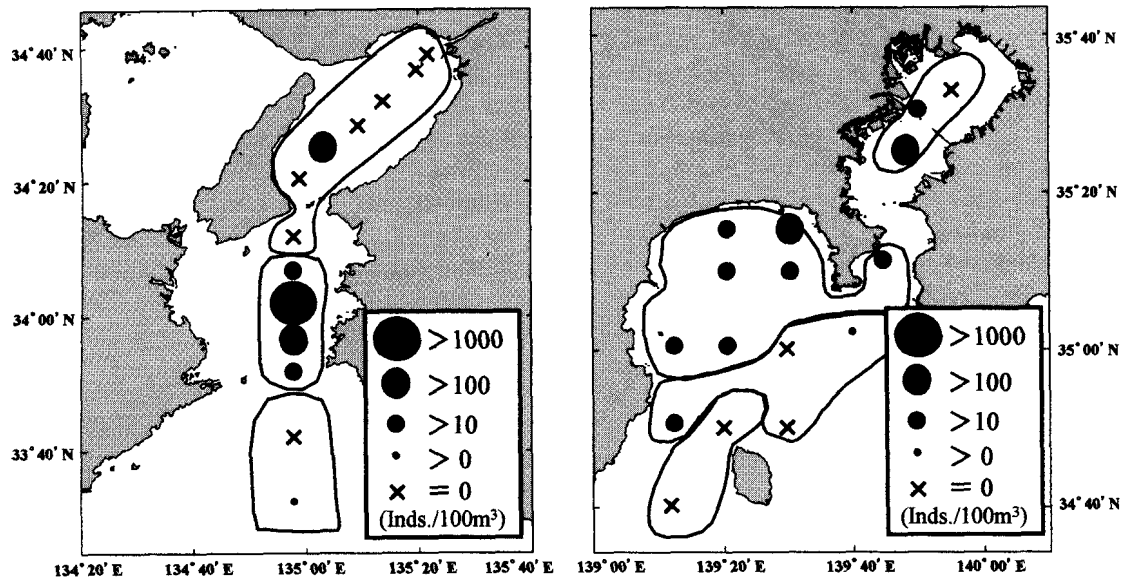


Fig. 5. Horizontal distributions of water masses and leptomedusan *Obelia* spp. in the Osaka Bay-Kii Channel area (left) and the Tokyo Bay-Sagami Bay area (right). Circles show population densities of this species (individuals per 100 m³).

most reach of Tokyo Bay. Eleven species of hydroidomedusae and 22 species of siphonophores were collected (Table 2). The number of species per station was small (less than five) within Tokyo Bay Water. On the other hand, the number of species was quite large in the Transitional water; 23 species at Stn. S4, 17 species at Stn. S11, and 19 species at Stn. S16.

Throughout the Tokyo Bay-Sagami Bay area, *Muggiaea atlantica* was the most numerous species (67% of the total number of individuals). It was collected from all the stations except the innermost two stations in Tokyo Bay (Stns. F2 and F3). This species was most abundant in Sagami Bay

Water and Transitional Water, but occurred at relatively low abundances (less than 10 inds./100 m³) in the two Oceanic Water stations (Fig. 4). The highest population density was recorded at Stn. S12 (1448 inds./100 m³). *Obelia* spp. were the second most abundant group (8% of the total number of individuals). The population density of *Obelia* spp. was high in Tokyo Bay Water, except Stn. F2, and Sagami Bay Water, but low or zero in Transitional Water and Oceanic Water (Fig. 5). The highest value was recorded at Stn. F6 (237 inds./100 m³). *Liriope tetraphylla* and *Aglaura hemistoma* were also dominant. Although the former was widely distributed in Sagami Bay, the population densities were

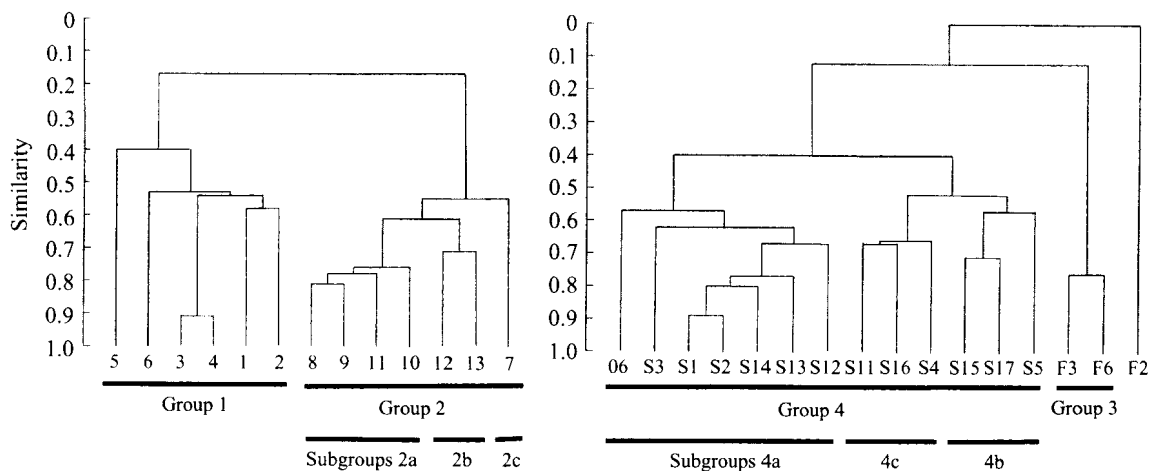


Fig. 6. Classification of cnidarian communities in the Osaka Bay-Kii Channel area (left) and the Tokyo Bay-Sagami Bay area (right). Scales on dendrograms correspond to percentage similarity coefficients.

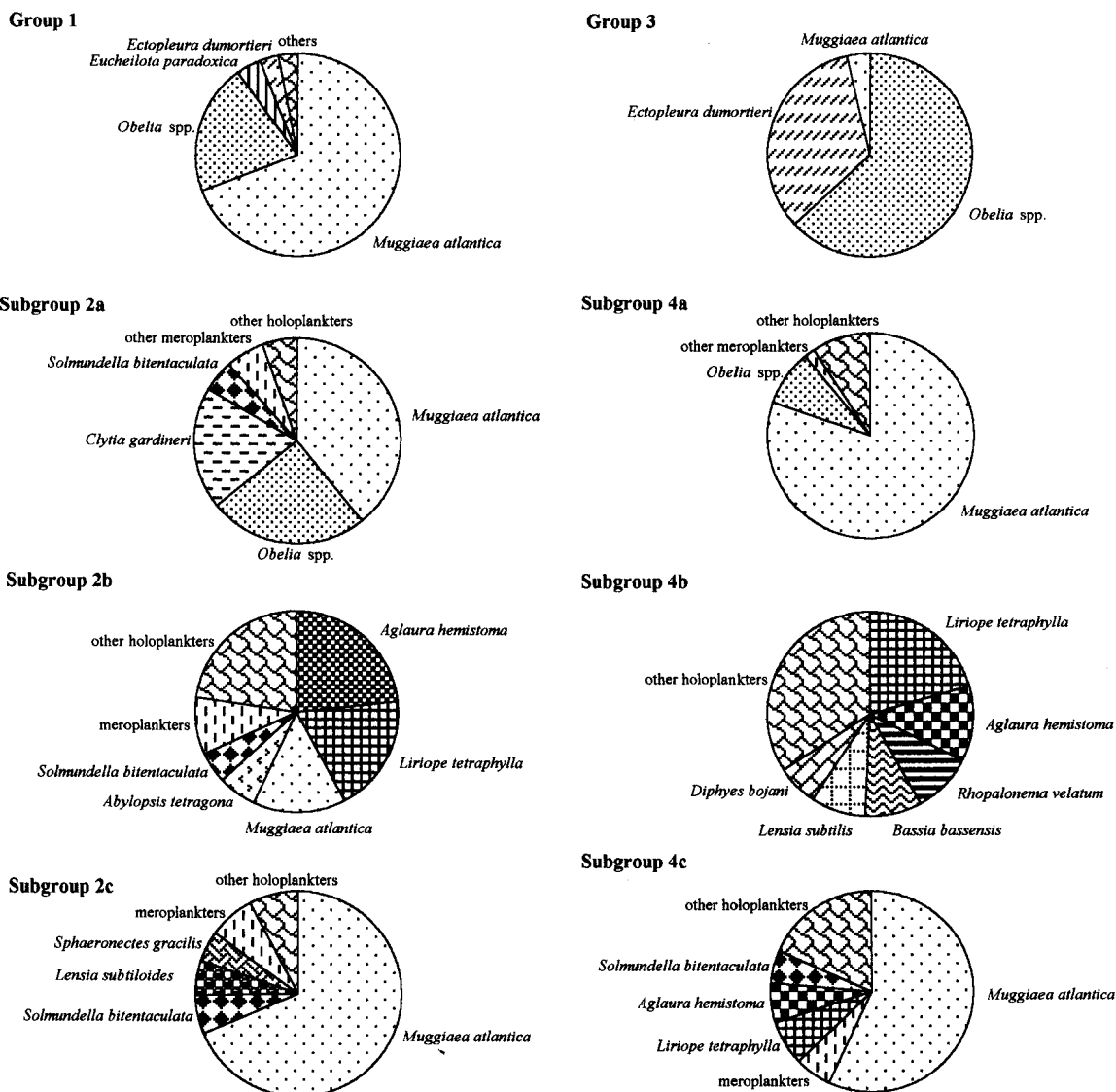


Fig. 7. Species composition of hydromedusan assemblages in the Osaka Bay-Kii Channel area and the Tokyo Bay-Sagami Bay area.

highest in Oceanic and Transitional Waters. The latter was also distributed widely in Sagami Bay. All siphonophore species apart from *M. atlantica* occurred at low population densities.

The cluster analysis distinguished two main groups at the 0.2 level of similarity, two stations in Tokyo Bay Water (F3, F6; Group 3) and all other stations (Group 4) except Stn. F2 (Fig. 6). Station F2 was ungrouped because no hydromedusae were collected. The hydromedusan assemblage of Group 3 was characterized an extremely low number of species (average 2.5 species per station). The dominant species in Group 3 were meroplanktonic *Obelia* spp. and *Ectopleura dumortieri* (Fig. 7). Group 4, which was characterized by the presence of a large number of species, could be divided further into three sub station groups at the 0.55 level of similarity (Fig. 6). Subgroup 4a consisted of six stations in northwestern Sagami Bay (Stns. S1–S3, S12–S14) and a station in southern Tokyo Bay (Stn. 06). Within the hydromedusan assemblage of Subgroup 4a, *M. atlantica* was the most numerous species (81% of the total abundance, Fig. 7). Meroplanktonic species such as *Obelia* spp. and *Eucheilota paradoxa* were also numerous. The average number of species per station was 9.7. Subgroup 4b included three stations (S5, S15, and S17); Stn. S5 was in the Transitional Water while Stns. S15 and S17 were in the Oceanic Water. The hydromedusan assemblage of Subgroup 4b was characterized as follows; (1) dominant species were trachymedusae such as *L. tetraphylla*, *A. hemistoma*, and *Rhopalonema velatum*, (2) ratio of siphonophores such as *Bassia*, *Diphyes* or *Lensia*, were high, (3) meroplanktonic species were absent, (4) no species occupied high percentages of the total abundance, and (5) the average number of species per station was 12.6 (Table 2, Fig. 7). The residual three stations (Stns. S4, S11, and S16) in Transitional Water were categorized as Subgroup 4c. Characters of the hydromedusan assemblage in Subgroup 4c were (1) number of species was large (average 18.3 species) and (2) although the most numerous species was *M. atlantica*, which accounted for 57% for the total individuals, this percentage was lower than that for Subgroup 4a (Table 2, Fig. 7). The species composition of this assemblage had an intermediate character between those of Subgroup 4a and Subgroup 4b.

Discussion

Effects of hydrographic conditions on the distributions of hydromedusan assemblages

According to Yoshioka (1985), Kii Channel is separated into two regions, the northern and southern, by a borderline defined by Gamoda Cape and Hino Cape. Hydrographic features are quite different in the two regions. When the Kuroshio Current flows directly eastwards to the south of Kii Channel, warm water generally flows up north along the Kii Peninsula and makes two counterclockwise circular flows in the northern and southern regions of the channel,

while lower salinity water discharged from Osaka Bay travels south along the eastern boundary of Shikoku Island.

During the present study, because the Kuroshio Current was flowing directly eastwards (Japan Maritime Agency 1997), water masses present in the Northern and Southern Kii Channel might be reflected the two counterclockwise circular flows. The highly saline Southern Kii Channel Water was more strongly influenced by the oceanic Kuroshio water than the lowly saline Northern Kii Channel Water.

Based on the cluster analysis, the Osaka Bay–Kii Channel area could be divided into four station groups. Distributions of these station groups corresponded well to those of the water masses. Group 1 was almost completely contained within Osaka Bay Water, whereas Subgroups 2a and 2b were found in the Northern and Southern Kii Channel Waters, respectively. Subgroup 2c was located in Stn. 7 where Osaka Bay Water existed at almost part of water column but Northern Kii Channel Water influenced bottom layer. The hydromedusan assemblage of Stn. 7, which was more similar to those of Kii Channel Waters, might be more strongly influenced by the bottom water.

Because Sagami Bay is only partially closed off from the Pacific Ocean, the hydrographic features there are complex. When the Kuroshio Current meanders around the Izu-ridge, oceanic water sometimes intrudes into Sagami Bay. The intrusion flows clockwise around Izu-Oshima Island; at the same time, the coastal water flows counterclockwise along the northern part of the bay (Otsuka 1972; Kawabe and Yoneno 1987). During the study period, path of the Kuroshio Current was winding west of the Izu-ridge and a strong inflow to Sagami Bay was observed through the Oshima West Channel (Japan Maritime Agency 1998). The highly saline Oceanic Water observed during this survey thus probably originated from the Kuroshio water, and the low salinity Sagami Bay Water was recognized as coastal water. The Tokyo Bay Water of lower temperature and lower salinity is probably formed due to the direct influence of river discharge.

Based on the hydromedusan assemblages, four station groups occurred in the Tokyo Bay–Sagami Bay area. Distributions of these station groups coincided with that of various water masses, as in the Osaka Bay–Kii Channel area. The Group 3 assemblage occurred within Tokyo Bay Water. In Sagami Bay, Subgroup 4a coincided with the Sagami Bay Water, Subgroup 4b included the Oceanic Water stations and the southernmost of the Transitional Water station. Subgroup 4c included the remaining three stations within Transitional Water.

As outlined above, the distribution of hydromedusan assemblages were related to those of water mass. The distribution of hydromedusae over coarse-scales is considered to be related to physical processes as indicated by many previous studies dealing with meso-scale (Goy 1973; Gili et al. 1991; Pagès & Gili 1991; Pagès 1992). Because lifetimes of oceanic physical phenomena change in direct proportion to their special scales (Mann & Lazier, 1991), coarse-scale

distributions of hydromedusae are supposed to fluctuate over shorter periods.

Characters of each hydromedusan assemblage

Hydromedusan assemblages belonging to Group 1 and Group 3, located in the semi-enclosed Osaka Bay and Tokyo Bay, respectively, had similar characters, such as a small number of species. Only two species of siphonophores occurred in these assemblages (*Muggiaea atlantica* and *Nanomia bijuga*) while many other siphonophore species were present in the other assemblages. Osaka Bay Water and Tokyo Bay Water were characterized by lower salinity. In the Gulf of Mexico, species numbers of siphonophores were also low at lower salinity stations (Gasca 1999). These results suggest that low salinities may inhibit the distribution of many siphonophore species.

Although *M. atlantica* was collected from all stations and was numerous in Osaka Bay, it was relatively scarce in the inner part of Tokyo Bay. Because Osaka Bay is connected to the Seto Inland Sea and the Kii Channel, water masses intruding into Osaka Bay through the channels are coastal ones, and contain large numbers of *M. atlantica*. On the other hand, exchange of water between Tokyo Bay and the outer ocean is not as prominent as in Osaka Bay (Unoki 1985). Differences in the occurrence patterns of *M. atlantica* between Osaka Bay and Tokyo Bay are probably due to factors such as the manner of water exchange.

Species number of meroplanktonic species were also low in the Osaka and Tokyo Bay assemblages. In Tokyo Bay, it is reported that eutrophication had made the zooplankton assemblages simpler (Nomura 1993; Uye 1994). In Scandinavian fjords, hydromedusan diversity decreased with increasing eutrophication (Arai 2001). Analogy leads us to think that eutrophic waters of Osaka Bay and Tokyo Bay may have been one of the major causes of the small diversity of meroplankters. The typical species that occurred in this assemblage were the meroplanktonic *Obelia* spp. and *Ectopleura dumortieri*.

The assemblage characteristics of Subgroups 2a and 4a, both located in coastal-featured water masses (Northern Kii Channel Water and Sagami Bay Water, respectively), were similar to each other. One of the similarities was the high abundance of *M. atlantica*. That this species was collected from almost all the stations proves its euryhaline nature. However, differences in the population density of *M. atlantica* were recognized among the stations; it was most numerous in Subgroups 2a and 4a (Fig. 4). Gili et al. (1988) reported that *M. atlantica* is distributed widely throughout the western Mediterranean, but that population densities differed according to local conditions. Higher abundance of this species in coastal waters has often been recorded (Gili et al. 1988; Pagès 1992). The other two siphonophores, *Lensia subtiloides* and *Sphaeroneustes irregularis*, are also recognized as coastal species because they mainly occurred in Subgroups 2a and 4a.

Another similarity between the coastal water mass stations was the large number of meroplanktonic species. These species were not collected in Oceanic Water. Large number of meroplanktonic species have been reported from Tanabe Bay, facing to Kii Channel (36 species; Yamazi 1958; Kubota 1995, 1997, 2000), and from the vicinity of Enoshima island, innermost part of Sagami Bay (22 species; Shimura et al. 1992). Of these species, at around half of this number were expected to occur in the present study period of early summer (Yamazi 1958; Horita 1996). In the present study, however, only six meroplanktonic species occurred at offshore stations in Subgroups 2a and 4a. Of these six species, four (*Clytia gardineri*, *Sugiura chengshanense*, *Podocoryne minima*, and *Eucheilota paradoxica*) are capable of asexual reproduction during the planktonic stages (Kramp 1961; Sugiura 1973; Hirano & Hirano 1997), the exception rather than the rule for meroplanktonic hydromedusan species. The former two undergo schizogenesis and the latter two produce medusa buds. These reproductive methods enable these species to increase population densities in offshore waters, although other meroplankters can reproduce only in nearshore waters because new medusae are as a rule released from benthic hydroids. On the other hand, *Obelia* species have not been reported to execute asexual reproduction during the planktonic stages. However, occurrence of *Obelia* spp. at oceanic stations, as in the present study, has sometimes been reported (Gili et al. 1991; Buecher & Gibbons 2000). Recruitment losses could be compensated for by the high productivity of this species (Gili et al. 1991). Because a single gonotheca of *Obelia* species produces numerous medusa buds (Kubota 1981), huge numbers of medusae may be released from benthic colonies. Only meroplanktonic species with unique life cycles such as these are probably able to spread their distributions into offshore waters. Life cycle characters are thus recognized to be biological factors that can influence hydromedusan distribution.

The Subgroup 4b assemblage contained no meroplanktonic species. Because this Subgroup was located in oceanic water intruding into Sagami Bay, all species were holoplanktonic, with many siphonophores and some of trachymedusae. Similar compositions were reported at oceanic stations in the Benguela current area (Pagès 1992) and off Chile (Pagès et al. 2001). Thus this type of composition is considered to be universal to oceanic hydromedusan assemblages.

The Subgroup 4c assemblage contained large numbers of species and had a species composition intermediate between those of Subgroups 4a and 4b. In Sagami Bay, meroplanktonic species occurred in Sagami Bay Water and Transitional Water, while many siphonophores occurred in Oceanic Water and Transitional Water. Characters of the Subgroup 4c assemblage, distributed in Transitional Water, were due to co-occurrence of coastal and oceanic species. The Subgroup 2b assemblage contained a large number of species and both meroplanktonic species and oceanic

siphonophores co-occurred. Thus this assemblage was also recognized to be of the transitional type. However, its character was more oceanic than that of Subgroup 4c because the composition of *M. atlantica* was only 16% although that in Subgroup 4c was over 50%, and furthermore other siphonophore species, such as *Abylopsis* or *Bassia*, were relatively numerous. Salinity of the water mass at station 12 was slightly higher than that at Subgroup 4c stations. It is likely that the above mentioned differences in species composition are due to differences in water characters.

As outlined above, similar distribution patterns of some hydromedusan assemblages were recognized in both study areas. The geographical distribution of hydromedusan assemblages depended on the geographical distribution of water mass while the type of assemblage was dependent on the physical characteristics of the water mass.

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References

- Alvariño, A. 1971. Siphonophores of the Pacific with a review of the world distribution. *Bull. Scripps Inst. Oceanogr., Univ. California, San Diego* **16**: 1–432.
- Arai, M. N. 2001. Pelagic coelenterates and eutrophication: A review. *Hydrobiologia* **451** (1/3): 69–87.
- Buecher, E. & Gibbons, M. J. 2000. Internal variation in the composition of the assemblages of medusae and ctenophores in St. Helena Bay, Southern Benguela Ecosystem. *Sci. Mar.* **64** (Supl. 1): 123–134.
- Gasca, R. 1999. Siphonophores (Cnidaria) and summer mesoscale features in the Gulf of Mexico. *Bull. Mar. Sci.* **65** (1): 75–89.
- Gili, J. M., Pagès, F. & Fusté, X. 1991. Mesoscale coupling between spatial distribution of planktonic cnidarians and hydrographic features along the Galician Coast (Northwestern Iberian Peninsula). *Sci. Mar.* **55**: 419–426.
- Gili, J. M., Pagès, F., Sabatés, A. & Ros, J. D. 1988. Small-scale distribution of a cnidarian population in the western Mediterranean. *J. Plankton Res.* **10** (3): 385–401.
- Goy, J. 1973. Note sur les Hydroméduses dans les eaux tropicales et subtropicales. *Bull. Mus. Natn. Hist. nat., Paris* **165**, Ecologie générale **21**: 333–343.
- Greeve, W. 1994. The 1989 German Bight invasion of *Muggiaea atlantica*. *ICES J. Mar. Sci.* **51**: 355–358.
- Hamner, W. M. & Schneider, D. 1986. Regularly spaced rows of medusae in the Bering Sea: Role of Langmuir circulation. *Limnol. Oceanogr.* **31**: 171–177.
- Hirano, Y. & Hirano, Y. 1997. Asexual reproduction performed by a pentamerous hydromedusa new to Japan. *Ann. Rep. Marine Ecosystem Res. Ctr., Chiba University* **17**: 3–5.
- Horita, T. 1996. Seasonal occurrence and unusual species of the medusae from adjacent waters of Toba in Mie Prefecture. *Aquabiology* **18** (2): 108–112. (in Japanese)
- Huntley, M. E. & Hobson, L. A. 1978. Medusa predation and plankton dynamics in a temperate fjord, British Columbia. *J. Fish. Res. Board Can.* **35**: 257–261.
- Japan Maritime Agency 1997. Quick Bulletin of Ocean Conditions, 1997, No. 12, Fig. 10.
- Japan Maritime Agency 1998. Quick Bulletin of Ocean Conditions, 1998, No. 13, Fig. 10.
- Kawabe, M. & M. Yoneno 1987. Water and flow variations in Sagami Bay under the influence of the Kuroshio path. *J. Oceanogr. Soc. Japan* **43**: 283–294.
- Kramp, P. L. 1959. The Hydromedusae of the Atlantic Ocean and adjacent waters. *Dana Rep.* **46**: 1–283.
- Kramp, P. L. 1961. Synopsis of the medusae of the world. *J. Mar. Biol. Assoc. U.K.* **40**: 1–469.
- Kramp, P. L. 1965. The Hydromedusae of the Pacific and Indian Oceans. *Dana Rep.* **68**: 1–161.
- Kramp, P. L. 1968. The Hydromedusae of the Pacific and Indian Oceans. Section II and III. *Dana Rep.* **72**: 1–200.
- Kubota, S. 1981. Life-history and taxonomy of an *Obelia* species (Hydrozoa; Campanulariidae) in Hokkaido, Japan. *J. Fac. Sci. Hokkaido Univ. Ser. VI, Zool.* **22** (4): 379–399.
- Kubota, S. 1995. Faunal list of Coelenterata collected from Tanabe Bay and its vicinities. Order Anthomedusae (Phylum Cnidaria, Class Hydrozoa). *Ann. Rep. Seto Mar. Biol. Lab.* **8**: 21–23. (in Japanese)
- Kubota, S. 1997. Faunal list of Coelenterata collected from Tanabe Bay and its vicinities. Order Leptomedusae (Phylum Cnidaria, Class Hydrozoa). *Ann. Rep. Seto Mar. Biol. Lab.* **11**: 31–32. (in Japanese)
- Kubota, S. 2000. Faunal list of Coelenterata collected from Tanabe Bay and its vicinities. Order Limnomedusae (Phylum Cnidaria, Class Hydrozoa). *Ann. Rep. Seto Mar. Biol. Lab.* **13**: 36–37. (in Japanese)
- Larson, R. J. 1987. Daily ration and predation by medusae and ctenophores in Saanich Inlet, B. C. Canada. *Neth. J. Sea Res.* **21** (1): 35–44.
- Mann, K. H. & Lazier, J. R. N. 1991. *Dynamics of Marine Ecosystems. Biological-physical Interactions in the Oceans*. Blackwell Scientific Publications, Boston, 466 pp.
- Motoda, S. 1957. North Pacific standard plankton net. *Inform. Bull. Planktol. Japan* **4**: 13–15. (in Japanese)
- Nomura, H. 1993. On zooplankton community structure and its temporal transition in the Tokyo Bay. *Ph. D. Thesis Tokyo Univ. Fish.* pp. 1–282. (in Japanese)
- Otsuka, K. 1972. On the influx of offshore water from the Kuroshio in the Sagami Bay based on the fluctuations of the daily mean sea level. *Bull. Japanese Soc. Fish. Oceanogr.* **20**: 1–12. (in Japanese)
- Pagès, F. 1992. Mesoscale coupling between planktonic cnidarian distribution and water masses during a temporal transition between active upwelling and abatement in the northern Benguela system. *S. Afr. J. Mar. Sci.* **12**: 41–52.
- Pagès, F. & Gili, J. M. 1991. Effects of large-scale advective processes on gelatinous zooplankton populations in the northern Benguela ecosystem. *Mar. Ecol. Prog. Ser.* **75**: 205–215.

- Pagès, F., González, H. E., Ramón, M., Sobarzo, M. & Gili, J. M. 2001. Gelatinous zooplankton assemblages associated with water masses in the Humboldt Current System, and potential predatory impact by *Bassia bassensis* (Siphonophora: Calyptophorae). *Mar. Ecol. Prog. Ser.* **210**: 13–24.
- Purcell, J. E. 1985. Predation on fish eggs and larvae by pelagic cnidarians and ctenophores. *Bull. Mar. Sci.* **37** (2): 739–755.
- Shimura, K., Takeshima, T., Adachi, A. & Tanimura, S. 1992. Breeding jellyfishes in Enoshima Aquarium. *J. Jap. Ass. Zool. Gard. Aqua.* **34** (4): 57–70. (in Japanese)
- Sugiura, Y. 1973. On the polyp and medusa of the hydromedusa, *Gastroblasta chengshanensis* Ling. *Publ. Seto Mar. Biol. Lab.* **20**: 209–220.
- Unoki, S. 1985. Tokyo Bay, II Physics, p. 344–361. In: *Coastal Oceanography of Japanese Islands* (ed. Coastal Oceanography Research Committee, The Oceanographical Society of Japan). Tokai Univ. Press, Tokyo. (in Japanese)
- Uye, S. 1994. Replacement of large copepods by small ones with eutrophication of embayments: cause and consequence. *Hydrobiologia* **292/293**: 513–519.
- van der Spoel, S. 1996. A hypothesis on Mesozoic vicariance in Hydromedusae. *J. Plankton Res.* **18** (4): 615–634.
- Whittaker, R. H. 1952. A study of summer foliage insect communities in the Great Smoky Mountains. *Ecol. Monograph* **22**: 1–44.
- Yamazi, I. 1958. Preliminary check-list of plankton organisms found in Tanabe Bay and its environs. *Publ. Seto Mar. Biol. Lab.* **7** (1): 111–163.
- Yoshioka, H. 1985. Seto Inland Sea I (A. Osaka Bay, B. Kii Channel), II Physics, p. 625–641. In: *Coastal Oceanography of Japanese Islands* (ed. Coastal Oceanography Research Committee, The Oceanographical Society of Japan). Tokai Univ. Press, Tokyo. (in Japanese)