Distribution and seasonality of sessile organisms on settlement panels submerged in Otsuchi Bay

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Abstract — Diversity and seasonal changes of the sessile organism assemblage in Otsuchi Bay (from 2013 to 2014) were surveyed by using moored settlement panels. Two barnacle species *Balanus trigonus* and *Megabalanus rosa* were remarkably abundant in summer. The barnacles showed different distribution patterns with depth; *M. rosa* tends to be abundant in 5–10 m deep, while *B. trigonus* was particularly abundant in deeper depths. More than 15 genera of encrusting bryozoans were obtained in Otsuchi Bay. The diversity of bryozoan genera was highest in summer–autumn; especially abundant in the southern inner-part of the bay. Botryllid colonial ascidians were abundant in autumn and early spring; especially abundant in the southern and inner-part of the bay. Most sessile organisms tended to be abundant in the southern part of the bay, where the outflow of the water current in the bay containing river water strongly affected. In the early spring, macroalgae tended to be abundant and sessile organisms decreased. Colonial organisms such as hydroids, colonial ascidians and bryozoans are considered to be primary colonizers on new substrates in Otsuchi Bay. Subsequent complex structures on substrates constructed by secondary colonizers such as barnacles and mussels provided the habitats for other organisms.

Key words: fouling organisms, barnacle, bryozoa, ascidian, assemblage, succession

Introduction

Sessile organisms attach to various substrates, such as rocks, algae and also artificial substrates. According to the rapid development and large abundance of sessile organisms on artificial floating substrates, they are well known as fouling organisms on port facilities, seawater intake facilities and ship bottom. Furthermore, many sessile organisms such as barnacles and bryozoans are filter-feeders; therefore, sessile organisms are also known as potential competitors to cultured oysters, scallops and ascidians.

The Sanriku Coast is part of the Pacific coast of the Tohoku Region, the northeastern Honshu Island, Japan. As the Sanriku Coast is influenced by both warm currents, the Kuroshio and the Tsugaru Current, and a cold current, the Oyashio Current, the area is famous for aquaculture fisheries of the oyster *Crassostrea gigas* (Thunberg 1793) and the scallop *Patinopecten yessoensis* (Jay 1857). Most of the aquaculture facilities along the Sanriku Coast were, however, heavily damaged by the Great East Japan Earthquake and the following massive tsunami on 11 March 2011. Although sessile organisms have been well known as fouling organisms on aquaculture facilities and cultured bivalves on the Sanriku Coast (Chida et al. 2011), the habitat environment for these sessile filter-feeders in this area might have been changed by the decrease of the cultured competitors and floating substrates. Therefore, studying and monitoring the amount and succession of sessile organisms after the tsunami provides fundamental information useful for the restoration of aquaculture in the area. Actual data on species composition and distribution of the sessile organisms will largely contribute to the appropriate prevention of the fouling organisms. Furthermore, observations of the seasonality and growth rate of sessile organisms with environmental investigation will enable us to determine the appropriate season for the prevention.

Monitoring the succession of sessile organisms on settlement panels is one of the easiest ways to study the diversity and seasonality of sessile organisms in natural environments (Hirata 1986, 1987, 1991). Although the communities of sessile organisms on mooring settlement panels are largely different from those on natural hard substrates (Glasby 1998, 2001, Glasby and Connell 2001), studying the succession of sessile organisms on panels provides fundamental information on the diversity and seasonality of sessile organisms on floating rafts and cultured bivalves (Ito and Kajihara 1988, Dziubińska and Janas 2007). Most settlement panel experiments use vertical positioning of the panels to avoid effects of sedimentation, however aquaculture facilities are three-dimensional in structure and the amount of fouling organisms may be different depend on the position due to the effect of sediment and/or light intensity.

Otsuchi Bay, located in the middle of the Sanriku Coast, is about 8km long by 2km wide, with three rivers flowing into the bay at the innermost part. The sessile organism fauna on ropes and settlement panels suspended from several floating rafts in the bay were previously studied by several researchers (Kajihara and Ura 1976, Kado et al. 1980), however the fauna has not been studied during the last 30 years. In this study, sessile organism diversity and their seasonality were surveyed by using mooring settlement panels at several localities in Otsuchi Bay, 1) to detail the sessile organism fauna and their seasonality after the 2011 tsunami, 2) to compare the amount of sessile organisms among different localities and depths, 3) to compare the amount of sessile organisms between the upper- and lower-surface of mooring substrates and 4) to estimate the succession pattern of sessile organisms on deployed objects in the bay.

Materials and Methods

The settlement panel series were deployed at six different localities in Otsuchi Bay on 7 August 2013 (Figure 1, Table 1). At each locality, a series of gray polyvinyl chloride (PVC) basal panels $(15 \text{ cm} \times 40 \text{ cm} \times 2 \text{ mm})$ were submerged at depths of 5 m, 10 m, 15 m and 20 m below sea level, set to keep the panels horizontal, with a logger for temperature and light intensity (HOBO Pendant Temperature/Light 64K Data Logger, UA-002–64, Onset) attached above each panel (Fig. 1). The loggers were set to measure the water temperature and light intensity at 15 minutes intervals. The transparent PVC settlement panels (15 cm×15 cm×2 mm) sandwich a part of upper- and lower-surface of the basal panel. Two pairs of the settlement panels were fixed to the basal panel at each depth with slide-clips; one of the pair was replaced every observation (approximately 3 months), and another pair was remained over twice the submerged periods (approximately 6 months).

The underwater panels were observed by SCUBA survey on 26 August 2013. The settlement panels were replaced every three months using the research boat Grand Maillet of the International Coastal Research Center (ICRC). Depth profiles of temperature, salinity and fluorescence were also observed at each locality just before the replacement using conductivity-temperature-depth (CTD) profiler (ASTD687, JFE Advantech, Japan, from August 2013 to February 2014; ASTD102, JFE Advantech, Japan, on 6 August 2014). In the following, each submerged period of settlement panels from deployment until replacement (from 7 August 2013 to 6, 7 November 2013; from 6, 7 November 2013 to 6, 7 February 2014; from 6, 7 February 2014 to 28 April 2014; and 28 April 2014 to 6 August 2014) are termed as "Season 1" to "Season 4," respectively (Table 1). The settlement panel series at three localities (Stations 1, 2 and 4) were deployed for one year. The other series (Stations 3, 5 and 6) were either damaged or lost due to winter storms; therefore, the series at these other localities were deployed only for the first season (Station 3) or first and second seasons (Stations 5 and 6).

Removed settlement panels were photographed from both surfaces using Nikon D7000 with AF-S Micro NIK-KOR 60 mm f/2.8G ED to identify the species and measure areas. Emcrusting bryozoan colonies were observed under



Fig. 1 Map showing the localities where the six settlement panel series were deployed, with the diagram of a settlement panel series.

Table 1.	Localities of the	deployed settlement	anel series.	Abbreviations for	the seasons:	Season 1; 7 Au	ıg. 2013–6,	7 Nov. 2	2013.
Season 2;	6, 7 Nov. 2013-6,	7 Feb. 2014. Seasor	1 3; 6, 7 Feb. 2	2014–28 Apr. 2014	. Season 4; 28	Apr. 2014–6 Au	g. 2014.		

Station	Locality	Longitude	Latitude	Depth	Surveyed season(s)
Station 1	Matsushima	39°20.726′N	141°55.032′E	24.4 m	1, 2, 3, 4
Station 2	Nagasaku	39°21.142′N	141°57.119′E	23.0 m	1,2, 3, 4
Station 3	Nagane	39°21.838′N	141°57.688′E	17.0 m	1
Station 4	Hiraiso	39°20.103′N	141°55.696′E	23.0 m	1, 2, 3, 4
Station 5	Nagasaki	39°20.423′N	141°57.792′E	24.5 m	1, 2
Station 6	Ohakozaki	39°20.936' N	141°59.167′E	23.3 m	1, 2

 Table 2.
 Measured characters for each taxon.

Таха	Observed characters
Porifera	number of individuals
hydroid (<i>Tubularia</i> sp.)	number of colonies
other hydroids	area
Barnacles	number of individuals
Bivalves	number of individuals
Spirorbidae sp.	area
(<i>Neodexiospira</i> sp.)	
other polychaetes	number of individuals
cheilostome bryozoa	area
(encrusting colonies)	
cheilostome bryozoa	number of colonies
(erect colonies)	
cyclostome bryozoa	number of colonies
ascidian (colonial)	area
ascidian (solitary)	number of individuals

stereomicroscopy to check the existance of ovicells and eggs. Subsequently, most species were removed from the panel, and appropriate characters for each taxon listed in Table 2 were measured. Areas were measured from digital photographs with ImageJ 1.37v software (Image Processing and Analysis in Java, Wayne Rasband, National Institutes of Health, USA; http://rsb.info.nih.gov/ij/). For the spirorbid polychaetes and hydroids, areas covered with their concentrated assemblages or stolonal networks (hydrorhiza) of colonies were approximately measured, and the area values were calculated from the rates of covering area on the panel. Dry weights were determined after 48-60 hours of drying in a drying oven at 70°C. In this study, the amount and distribution of sessile organisms within a settlement panel was not assessed; therefore, edge effects were not considered in the analyses. To avoid the effect of secondary coverage by sessile organisms attached to the settled organisms in the analyses of the amount of primary settled organisms, only organisms attached directly to the panel were used for each analyses. Sessile organisms attached to the settled organisms were analysed separately as secondary colonizers. The results of the diversity and amount of sessile organisms were compared between the depths (5, 10, 15 and 20 m), localities and submerged periods (Seasons 1-4).

To group the localities with similar species compositions, we conducted two methods of cluster analyses based on the species composition and abundance of the first two seasons (Seasons 1 and 2) using R version 3.2.3 software (R Development Core Team 2011). For the first clustering, we started with the Euclidean distance, and implemented the Ward's hierarchical clustering method. For the second clustering, we started with the Bray-Curtis dissimilarity analyses based on the species composition of five localities to avoid the lacking data of Station 3. The results were implemented a group average clustering method.

All examined specimens have been deposited in ICRC



Fig. 2 Annual changes in water temperature at different depths in Otsuchi Bay. Each value at all examined stations are shown together in a single graph.

Table 3. Ranges of water temperature at different depths in each season. MRT indicates the mean range of temperature for each season.

Aug.–Oct.	Nov.–Jan.	Feb.–Apr.	May–Jul.		
4.04–24.35	6.88–17.38	2.62-8.08	4.31-21.00		
6.81–23.87	6.27-17.09	2.52-8.18	4.31–19.57		
5.76-23.20	7.18–17.00	2.41-8.08	4.10-19.28		
5.28–23.10	7.48–16.90	2.52-8.08	4.31-19.19		
8.1575	10.14	5.5875	15.5025		
	AugOct. 4.04-24.35 6.81-23.87 5.76-23.20 5.28-23.10 8.1575	AugOct. NovJan. 4.04-24.35 6.88-17.38 6.81-23.87 6.27-17.09 5.76-23.20 7.18-17.00 5.28-23.10 7.48-16.90 8.1575 10.14	AugOct. NovJan. FebApr. 4.04-24.35 6.88-17.38 2.62-8.08 6.81-23.87 6.27-17.09 2.52-8.18 5.76-23.20 7.18-17.00 2.41-8.08 5.28-23.10 7.48-16.90 2.52-8.08 8.1575 10.14 5.5875		

with the registration number of BORAS (TEAMS Biological Observation Record Archive System) from 7425 to 7599.

Results

Environment characters

The water temperature in Otsuchi Bay ranged from 2.4°C to 24.4°C; the annual range of water temperature during the survey was about 22°C. Short term fluctuation ranges of the water temperature in Seasons 1 and 4 were larger than those in Seasons 2 and 3 (Fig. 2); the ranges increased greatly with increasing depth. Mean range of the water temperature in Season 3 (5.6°C) was smallest and that in Season 4 (15.5°C) was largest (Table 3). The temporal difference in water temperature between the stations was largest (1.5–3.5°C) in Season 1; the highest at Station 2, and lowest at Station 1. No significant differences were found in the ranges and mean values of water temperature between the different stations and different depths in each season.

Salinities at all the depths of settlement panels were generally within the range from 33.3 to 33.8 in most observations (Fig. 3). Generally, lower salinities were observed at shallower than 4 m deep. Although the salinities at 5 m deep were slightly lower than the values at other depths, there were no remarkable differences between the depths of settlement panels at the time of our observations. Salinities at the end of April were exceptionally lower than those in the other



5 m 10 m 15 m 20 m 5 m 10 m 15 m 20 m

Fig. 3 Salinities at each examined depth among the surveyed stations.



Fig. 4 Fluorescence profiles at each stations in different seasons.

seasons; ranged from 32.6 to 32.9 (Fig. 3).

Fluorescence profiles of the observations shows slightly higher values at stations located inner and southern part of the bay (Stations 1, 4 and 5) in late August (Fig. 4). The values at 5–10 m deep at stations located in the northern part of the bay (Stations 2 and 3) were lower than those at 15–20 m deep. Subsequently, increased fluorescence values were observed at 5 m deep at stations located in the inner and southern parts of the bay (Stations 1, 4, 5 and 6) in early November. Fluorescence values remarkably increased at all stations in early February; the values at 10–15 m deep also increased. However, fluorescence values in the northern part of the bay (Station 2) was slightly lower than those in the inner and southern parts. The highest fluorescence values at each station were observed at 10–20 m deep at the end of April (Fig.



Fig. 5 Integrated light intensity values for 10 days (from 8 to 17 August 2013) at each stations. † indicates lack of data at 15m and 20m depth.

4). Finally, fluorescence values decreased at all the depths at all stations in early August.

Light intensities were compared between the localities and depths with 10 day cumulative values (Fig. 5). To avoid the effects by sessile organisms and algae on the logger surfaces, only 10 day data for immediately after the logger was deployed were used for the study. The results show that lower values occurred in the inner part of the bay (Stations 1 and 4). The values at northern localities (Stations 2 and 3) are higher than those at the southern localities (Stations 4, 5 and 6). The cumulative light intensity at each surveyed depth decreased by half for increasing every 5 m deep.

Species composition and seasonality of sessile organisms in Otsuchi Bay

In total, more than 52 species belonging to seven phyla were obtained from the settlement panels in Otsuchi Bay (Table 4, Fig. 6). There were only few organisms observed on the panels during the underwater observations of three weeks after deployment; only hydroids were found on the panels at Station 3, and colonial ascidians at Station 4. Subsequently, on most panels settlement of large amount of barnacles (Megabalanus rosa Pilsbry, 1916 and Balanus trigonus Darwin, 1854) and various bryozoans occurred during summer and autumn. Encrusting bryozoa Pacificincola sp. had some empty ovicells in Season 1 (Fig. 7A). In Season 2, the number of barnacles remarkably decreased, and encrusting bryozoans and colonial ascidians replaced barnacles. Encrusting bryozoa Pacificincola sp., however, had no ovicells during this season (Fig. 7B). Some macroalgae (Rhodophyceae, Ulvophyceae and Phaeophyceae) were found on panels at shallow depths in this season (Table 4). Colonial ascidians often overgrew the barnacles on the panels submerged over two periods of Seasons 1 and 2. Terebellid polychaetes, some species of molluscs (e.g., Musculus cf. nipponicus) and some solitary ascidians (Ciona savignyi Herdman, 1882 and Styela clava Herdman, 1881) were also remarkably abundant on the panels submerged over two periods of Seasons 1 and 2. During winter in Season 3, macroalgae tended to be abundant, and the total amount of sessile organisms remarkably decreased. Subsequently, colonial ascidians became abundant in Season 4. Some encrusting bryozoans were found in this season; Pacificincola sp. had a large amount of ovicells with embryos inside (Fig. 7C). Megabalanus rosa also started to settle during early spring in Season 4. Colonial ascidians were abundant on the panels submerged over two periods of Seasons 3 and 4. Large numbers of the solitary ascidian C. savignyi were also found in Season 4.

Cluster analyses based on the species composition and abundance of sessile organisms in the first two seasons (Seasons 1 and 2) showed four major clusters (Fig. 8). The resulting two cladograms were almost identical in topology, except Station 1 appeared as separated from all other stations in the Bray-Curtis dissimilarity analyses. One cluster contains Stations 2 and 6 located in the middle to entrance of the bay; the localities in this cluster are characterized by facing an opened space in the bay (Fig. 1). Another cluster contains Stations 3 and 5 located in the entrance of the bay; the localities in this cluster are characterized with the area in recess beside a small cape (Fig. 1). Stations 1 and 4 in the inner part of the bay comprises the separate two clades in the analyses, respectively.

Amount of each taxon at different localities and depths

Sponges

Only few sponges were obtained in Seasons 1 and 2 (Table 4). The amount of sponges was remarkably small in all the seasons throughout this study.

Hydroids and other cnidarians

Several colonies of *Tubularia* sp. were obtained at 5–10 m deep at most stations except in the inner part of the bay in Season 1 (Table 4). The other hydroid colonies occurred at most stations; especially abundant at 15–20 m deep. Hydroids were also obtained in Season 3, but decreased in Season 4.

Few sea anemones were obtained from the panels at Stations 4 and 5 in Season 1, and also from the panels submerged over two periods of Seasons 3 and 4 (Table 4).

Barnacles

Barnacles were remarkably abundant in Season 1; B. trigonus (Fig. 6B) and M. rosa (Fig. 6A) were the most abundant species (Table 4). Both species were, however, less abundant at Station 1 (Fig. 9), and M. rosa was also less abundant at Station 4, compared to the other stations. Balanus trigonus was especially abundant at 15-20m deep, in contrast to M. rosa which was abundant at 5-10m deep (Figs. 9, 10). The remarkably small amount of B. trigonus at Station 3 is probably owing to the loss of panels at 15 m and 20 m deep in the locality (Fig. 9). We conducted the Kruskal-Wallis test and the subsequent Mann-Whitney test with the post hoc Bonferoni method for the number and dry weight of barnacles between the depths with combined the data for each depth, avoid the outliers shown in the box plot (Fig. 10). The results of the test showed that the number of B. trigonus was significantly more at 15 m deep compared to 5 m deep. The results also showed that the number of M. rosa was significantly more at 10m deep compared to 20m deep. A similar tendency was also shown in the amount of dry weight of both species at each depth, and moreover the dry weight of M. rosa at 5 m deep was also significantly more compared to 20 m deep (Fig. 10). The calculated growth rates (dry weight per individual) of barnacles were higher at shallower depths. The results showed the growth rates of B. tri-

Season				1	2	3	4	1–2	3–4
Number of surveyed stations				6	5	3	3	5	3
Number of examined panels				43	36	22	24	32	24
Porifera		Demospongiae spp.	NI	1	1	0	0	3	0
Cnidaria	sea anemone	Actiniaria (sea anemone)	NI	2	0	0	0	0	1
omaana	hydroid	Tubularia sp	NI	131	0	0	0	0	0
	nyarola	other hydroid (<i>Obelia</i> spp.)	Δ	205	1521	353	130	_	335
Crustacea	harnacle	Balanus trigonus	NI	5053	15	000	15	2662	000
orastacca	barnaele	Dalanas ingonas		176	15	0	1~	190	0
		Megabalanus rosa	NI	1/2/	/1	0	137	169	100
		Wegabalands rosa		643	15	0	107	378	100
		Semibalanus cariosus	NI	0+0	0	0	0	0,0	1
		Balanus crenatus	NI	0	15	0	0	0	0
		Balanus improvisus	NI	0	0	0	2	0	52
		Fistulobalanus albicostatus	NI	0	1	0	0	0	1
		unidentified barnacle	NI	0	0	1	0	1	3
	amphinod		NI	210	2	0	0	4	0
Mollussa	bivalvos		NI	210	5	0	2	43	6
WOIlusca	Divalves	Anomia of obinancia	NI	70	2	0	ے 1	57	0
		Anomia Ci. Chinensis	NI	110	2	0	0	420	0
		Ptorio op		110	0	0	0	430	0
		Chlorence an	INI NU	1	0	0	0	1	0
		Chianys sp.		1	0	0	3	10	9 17
A	Dalvalaata	<i>Modolus</i> sp.		405	2	0	ГС		17
Annelida	Polychaeta	Spirorbidae sp. (<i>Veodexiospira</i> sp.) Serpulidae sp. (<i>Protohydroides/</i>	A	405	372	0	00	001	74
		Hydroides)	NI	270	18	0	1	619	0
		Terebellidae sp.	NI	1	16	0	0	355	0
		other polychaetes	NI	19	1	0	0	26	0
Bryozoa	encrusting								
	Cheilostomata	in total	A	413	432	3	92	380	82
	erect								
	Cheilosotmata	<i>Beania</i> sp.	NI	1	0	0	0	0	0
		Tricellaria occidentalis	NI	71	2	0	0	78	7
		Bugulina californica	NI	3	1	3	5	1	6
	Cyclostomata	<i>Lichenopora</i> spp.	NI	0	0	0	2	2	3
		<i>Tubulipora</i> spp.	NI	0	7	0	4	21	3
Chordata	solitary ascidian	Ciona savignyi	NI	67	6	0	235	161	186
		Corella japonica	NI	0	31	0	13	3	17
		Pyuridae sp. 1	NI	10	1	0	0	0	0
		Pyuridae sp. 2	NI	0	0	0	1	0	0
		Styela clava	NI	0	0	0	0	359	1
		Styelidae sp.	NI	0	0	0	0	25	0
	colonial ascidian	Botryllidae sp. 1	A	139	677	96	1420	_	2021
		Botryllidae sp. 2	A	13	24	0	0	—	0
		Botryllidae sp. 3	А	18	44	0	0	—	0
		Botryllid ascidian Total	А	170	745	96	1420	—	2021
		<i>Didemnum</i> sp.	А	0	24	0	157	—	206
Ulvophyceae		<i>Ulva</i> sp.	NP	0	3	0	2	2	0
		<i>Cladophora</i> sp.	NP	0	1	0	0	0	0
Phaeophyceae		Undaria pinnatifida	NP	0	0	0	0	1	2
		Saccharina religiosa	NP	0	0	0	0	0	4

NP

NP

NP

NΡ

Ectocarpus sp.

Gigartinales spp.

Ceramiales spp.

Rhodophyceae

Colpomenia cf. sinuosa

Table 4. Obtained sessile organisms. Abbreviations: A, total area (cm²); DW, total dry weight (g); NI, total number of individuals; NP, total number of panels.



Fig. 6 Sessile organisms obtained in this study. A, *Megabalanus rosa* (barnacle); B, *Balanus trigonus* (barnacle); C, *Tubularia* sp. (hydroid); D, Spirorbidae (polychaete); E, *Anomia* cf. *chinensis* (mollusc); F, *Electra* sp. (encrusting cheilostome bryozoa); G, *Bugulina californica* (erect cheilostome bryozoa); H, *Ciona savignyi* (solitary ascidian); I, *Corella japonica* (solitary ascidian) seen from the ventral side; J, Botryllidae sp. 1 (colonial ascidian); K, Botryllidae sp. 2 (colonial ascidian); L, Botryllidae sp. 3 (colonial ascidian).



Fig. 7 Colonies of Pacificincola sp. obtained in different seasons. A, Season 1; B, Season 2; C, Season 4.



Fig. 8 Dendrogram of cluster analyses by Euclidean distance analyses (left) and Bray-Curtis dissimilarity analyses (right), between the stations based on the species composition in Season 1 and 2.



Fig. 9 Depth distributions of two barnacle species *Balanus trigonus* and *Megabalanus rosa*, at each station in season 1. † indicates lack of data at 20 m upper-surface; ‡ indicates lack of data at 15 m and 20 m deep.



Fig. 10 Box plots of settlement tendency of two barnacle species *Balanus trigonus* and *Megabalanus rosa*, for each examined depth, based on the number of individuals (A), dry weights (B) and estimated growth rates (C), respectively. The bottom and top of the box indicate 25th and 75th percentiles, respectively. The line inside the box indicates the median. The bottom and top of the bar indicate the lowest and highest values within 1.5 x IQR of the lower and upper quartile, respectively. The outliers are shown as outlined plot. Asterisks indicate the statistical significance (p<0.05) in the Kruskal–Wallis test with the post hoc Bonferoni method.

gonus was significantly higher at 5 m, and that of *M. rosa* was significantly higher at 5 m and 10 m deep compared to 20 m deep, which were supported by the Mann–Whitney test.

The number and dry weight of barnacles were also compared between the upper- and lower-surfaces at each depth (Fig. 11). We conducted the Brunner-Munzel test for the number and dry weight of barnacles between the upper- and lower-surfaces, avoid the outliers shown in the box plot (Fig. 12). The differences between upper- and lower-surfaces in both *M. rosa* and *B. trigonus* (Figs. 11, 12) were not significant in the Brunner-Munzel test but slightly larger on the lower-surface. There were no significant differences in the growth rate of barnacles between the upper- and lower-surfaces except that of *M. rosa* at 5 m deep (Fig. 11).

Other barnacles were not as abundant as the former two species (Table 4). *Balanus crenatus* Bruguière, 1789 were

obtained from various depths at most stations (Stations 1, 2, 5 and 6) in Season 2. *Balanus improvisus* Darwin, 1854 was the most abundant at 15 m deep at Station 2 on the panels submerged over two periods of Seasons 3 and 4 (Table 4); this species was also obtained from 15–20 m deep at Stations 1 and 4 in the same seasons. Only single specimens of *Semibalanus cariosus* (Pallas 1788) and *Fistulobalanus albicostatus* (Pilsbry 1916) were obtained from Station 4 on the panels submerged over two periods of Seasons 3 and 4. Another specimen of *F. albicostatus* was also obtained from Station 4 in Season 2.

Amphipods

A large amount of tubes formed by ischyrocerid amphipods were found on the settlement panels at Station 1 in Season 1 (Table 4). They were also obtained from the panels at

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Fig. 11 Cumulative number of individuals and dry weights of two barnacle species *Balanus trigonus* and *Megabalanus rosa*, that appeared on the upper- and lower-surfaces of the settlement panels in season 1. Asterisk indicates the statistical significance (p < 0.05) between upper- and lower-surface in the Brunner–Munzel test.



Fig. 12 Box plots of settlement tendency of two barnacle species *Balanus trigonus* and *Megabalanus rosa*, for upper- and lower-surface of the panels, based on the number of individuals (A), dry weight (B) and the estimated growth rates (C), respectively. The outliers are shown as outlined plot.

Station 1 submerged over two periods of Seasons 1 and 2.

Molluscs

Mytilus galloprovincialis Lamarck, 1819 were obtained from 5–10 m deep at Stations 4 and5 in Season 1. They were

also obtained from same localities, on the panels submerged over two periods of Seasons 1 and 2. *Anomia* cf. *chinensis* were abundant in Season 1; they were obtained from 10–20 m deep at stations in the middle and entrance of the bay (Stations 2, 5 and 6). *Pteria* sp. were obtained from Station 2 in Season 1. *Chlamys* sp. were obtained from Station 2 in Season 1 and from all stations (Stations 1, 2 and 4) in Season 4. *Modiolus* sp. were obtained from Station 2 (Season 2) and Station 4 (Season 4), and were much more abundant on the panels submerged over two seasons at Station 4 (Table 4). A large amount of *Musculus* cf. *nipponicus* was obtained from 5–15 m deep at stations in the middle and entrance of the bay (Stations 2, 3, 5 and 6) in Season 1 (Table 4). *Musculus* cf. *nipponicus* were remarkably abundant at 5–10 m deep at Station 5, on the upper-surface of the panels submerged over two periods of Seasons 1 and 2.

Polychaetes

Serpulid polychaetes were obtained from most stations deeper than 10 m in Season 1. The serpulid polychaetes were also abundant on panels submerged over two periods of Seasons 1 and 2 (Table 4), and the amount was especially large at 15–20 m deep. Spirorbid polychaetes were obtained in most seasons except Season 3; especially abundant in Seasons 1 and 2 (Table 4). The abundance of spirorbid polychaetes was high at stations in the inner part of the bay (Stations 1 and 4) in all the seasons. Moreover, they were also abundant at 20 m deep at Station 2 in Season 4. Spirorbid polychaetes were abundant on the lower-surface of the panels submerged over two periods of Seasons 1 and 2, at every depth at Station 1. The other polychetes were obtained from 5–10 m deep at stations in the inner and northern parts of the bay (Stations 1, 2 and 3) during Seasons 1 and 2 (Table 4).

Bryozoans

Bryozoans were abundant in Season 1 and Season 2.

Erect species, Tricellaria occidentalis (Trask 1857) and Bugulina californica (Robertson, 1905), were abundant at the depth ranges 5-15 m at Stations 3 and 4 (Table 4). A similar tendency was also observed on the panels submerged over two periods of Seasons 1 and 2. A small colony of Beania sp. was obtained from 10m deep at Station 2 in Season 1. Encrusting bryozoans were especially abundant; more than 15 genera were obtained (Figs. 13 and 14). The diversity of encrusting cheilostome bryozoan genera was highest in Season 1 and Season 2 with 11 genera and 9 genera, respectively (Fig. 14). The amount of bryozoan colonies was lowest in Season 3; only a single genus Pacificincola was obtained. Eight genera were obtained in Season 4; species composition was different from the other seasons as Microporella, Callopora and Celleporella were also abundant in this season (Fig. 14). Four genera, Pacificincola, Celleporina, Electra and Exochella were abundant in most seasons (Figs. 13 and 14). Both encrusting and erect bryozoan colonies were most abundant at Station 4 (Fig. 14). There were no significant differences in the bryozoan species composition among the surveyed stations.

Total encrusting area of cheilostome bryozoans was compared between the seasons (except Season 1); the encrusting area was the largest at Station 4 in Season 2 (Fig. 15). Some large colonies of encrusting bryozoans were obtained at 5–10 m deep; *Electra*, *Pacificincola* and *Celleporina* were dominant. *Electra* and *Exochella* also occurred at 15 m deep at Stations 5 and 6. *Exochella* was especially abundant at 15 m deep. The total encrusting area of bryozoans at Station 4 remarkably decreased in Seasons 3 and 4 (Fig. 15).



Fig. 13 Some of the obtained encrusting cheilostome bryozoans in Otsuchi Bay. A, *Pacificincola* sp.; B, *Electra* sp.; C, *Celleporina* sp.; D, *Exochella* sp.; E, *Microporella* sp.; F, *Celleporella* sp.; G, *Callopora* sp.; H, *Smittoidea* sp.; I, *Fenestrulina* sp.

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Fig. 14 Species composition of encrusting cheilostome bryzoan genera in each season. The number of examined settlement panels are indicated at the top of each histogram. The number of examined stations are indicated in parentheses following the number of panels.



Fig. 15 Depth distribution of encrusting cheilostome bryozoans at each station in each season. x indicates lack of data.

Cyclostome bryozoans were not as abundant as cheilostomes. *Lichenopora* spp. were obtained from 10–15 m deep at Stations 2 and 4 in Season 4. *Lichenopora* spp. were also obtained from 20m deep at Stations 6 and 1, on the panels submerged over two periods of Seasons 1–2 and Seasons 3–4, respectively (Table 4). *Tubulipora* spp. were obtained from Station 2 (20m deep) and Station 6 (10–20m deep) in Season 2, and Station 1 (20m deep) and Station 2 (15–20m deep) in Season 4. *Tubulipora* spp. were also obtained from Station 1 (15m deep) and Station 2 (15–20m), on the panels submerged over two periods of Seasons 3 and 4. *Tubulipora* spp. were also obtained from Station 1 (20m deep), on the panels submerged over two periods of Seasons 1 and 2.

Colonial ascidians

Botryllid ascidians were abundant in Season 2 and Season 4; especially dominant in Season 4 (Table 4). Total encrusting area of botryllid ascidians was compared between the seasons (except Season 1); the area was significantly smaller at Station 2 compared to the other stations, in all seasons throughout the survey (Fig. 16). In contrast, the area of botryllid ascidians was large at inner and southern part of the bay (Stations 1, 4, 5 and 6). Botryllid ascidians were especially abundant at 5–10m deep in all seasons (Fig. 16).

Didemnum sp. was also obtained from 5 m deep at Station 5 in Season 2 and Station 4 in Season 4 (Table 4). A similar tendency was also observed on the panels submerged



Fig. 16 Depth distribution of botryllid ascidians at each station in each season. x indicates lack of data.



Fig. 17 Schematic diagram of the succession of sessile organisms on mooring settlement panels in Otsuchi Bay. A, settlement of colonial organisms such as hydroids, botryllid ascidians and encrusting bryozoans in early stage; B, settlement of solitary organisms such as barnacles and mussels in intermediate stage; C, overgrown by the colonial ascidians and/or macroalgae in later stage; D, renewal settlement by sessile organisms using empty space and skeleton of dead barnacles.

over two periods of Seasons 3 and 4; *Didemnum* sp. was abundant from 5 m deep at Station 4.

Solitary ascidians

Most solitary ascidians were found at the lower-surface of panels. *Ciona savignyi* were abundant at 5–10 m deep at stations in the southern part of the bay (Stations 4, 5 and 6) in Season 1. *Ciona savignyi* were also abundant in Season 4; more than 200 individuals were obtained from the lower-surface at 15 m deep at Station 1 (Table 4). A similar tendency was observed on the panels submerged over two periods of Seasons 3 and 4; more than 170 individuals were obtained from the lower-surface of the panel at 15 m deep at Station 1.

Styela clava were abundant on the panels submerged over two periods of Seasons 1 and 2 (Table 4). *Styela clava* were especially abundant at 5–10 m deep at stations in southern part of the bay (Stations 4, 5 and 6) and on lower-surface of the panel at 10 m deep at Station 5; more than 300 individuals were obtained.

Corella japonica Herdman, 1880 were obtained from Station 1 in Season 2, and from Stations 1 and 2 in Season 4 (Table 4). *Corella japonica* were especially abundant on lower-surface of the panels at 15 m deep at Station 1 in Season 2; more than 20 individuals were obtained. A similar tendency was also observed on the panels submerged over two periods of Seasons 3 and 4; more than 10 individuals were obtained from the lower-surface of the panel at 15 m deep at Station 1.

The other solitary ascidians were obtained from the lower-surface of the panels at 15 m deep at Station 4 (Season 1) and Station 5 (Season 2). The small reddish young ascidians Styelidae sp. were obtained from the panels at 10–15 m deep at Stations 5 and 6 submerged over two periods of Seasons 1 and 2 (Table 4).

Discussion

Differences in the species composition from previous reports

Sessile organism diversities on mooring culturing facilities and seawalls in Otsuchi Bay have been previously studied in 1976 (Kajihara and Ura 1976). Some species obtained in the present study (e.g., most species of barnacles) are common with the previous reports (Kajihara and Ura 1976, Kado et al. 1980). Distribution of the serpulid polychaetes in the present study corresponds to that of *Hydroides ezoensis* Okuda, 1934 previously reported from culturing facilities in July 1974 (Kajihara and Ura 1976); they were abundant in the inner part and southern part of the bay. Solitary ascidian *S. clava* was obtained from only southern part in the bay; it also corresponds to the area where *S. clava* was previously reported (Kajihara and Ura 1976).

On the other hand, some species reported in the previous studies (e.g., Chthamalus challengeri Hoek, 1883) were not obtained in the present study. Previous studies surveyed at shallower depths such as 1m deep and intertidal zones, where the species composition is supposed to be largely different from the compositions examined at subtidal deeper depths in the present study. Therefore, the absence of these species is likely to be due to their specific distributions at shallower depths. Difference of the substrates may be another possible factor. Chthamalus challengeri, for example, was found to be abundant on stable seawalls (Kajihara and Ura 1976), while M. rosa prefers moored substrates such as settlement panels (Yamaguchi 1977). Mytilus galloprovincialis is one of the common fouling organisms on buoys and ropes in Otsuchi Bay (Kajihara and Ura 1976); they were abundant in the southern part of the bay (Stations 4 and 5), but less abundant on the settlement panels than ropes and buoys at same locality in the present study. This was probably caused by the preference of substrates by M. galloprovincialis.

The bryozoan fauna on mooring structures in Otsuchi Bay is largely different from the previous report (Kajihara and Ura 1976). Although Bugulina californica was the only bryozoan species previously reported on mooring objects in Otsuchi Bay (Kajihara and Ura 1976), the bryozoan fauna is characterized by various encrusting species in the present study. Pacificincola sp. was common at most localities throughout all seasons in this study, and some other encrusting cheilostome species, Electra sp., Celleporina sp. and Exochella sp., were also abundant in most seasons except Season 3 (Fig. 14); therefore, these species appear to be representative bryozoans on the settlement panels in Otsuchi Bay. In contrast, erect bryozoans were not abundant in Otsuchi Bay throughout the survey periods of the present study; the most abundant species obtained in the present study was T. occidentalis, which is one of the common species on mooring substrates reported in Japan.

Differences in the species composition among stations

The results of cluster analyses based on the species composition and abundance of sessile organisms in the first two seasons (Seasons 1 and 2) showed four clusters which were characterized by different oceanographic features (Fig. 8). Although there were no remarkable differences in temperature and salinity between the stations, all the clusters obtained do not contain the two adjacent stations, indicating that the species composition and abundance of sessile organisms could be different even between close localities. The results of the cluster analyses also indicate the significant differences in species composition between the inner part and the mouth of the bay. Species abundance of sessile organisms changes depending on the movement of substrates (Glasby 2001), and the oceanographic features are related to the difference in water flow; therefore, the species composition and abundance of sessile organisms are probably characterized by the feature of water flow at the localities in Otsuchi Bay.

Colonial ascidians appeared abundantly in Seasons 2 and 4, however the amount of colonies was significantly less abundant in Station 2 compared to the other stations during both seasons (Fig. 16); the distribution of colonial ascidians concentrated in the inner and southern part of the bay (Stations 1, 4, 5 and 6). The distribution pattern of the colonial ascidians corresponds to the area affected by low salinity water in the bay from river water from April to October (Otobe et al. 2009, Ishizu et al. 2016). The most abundant season of colonial ascidians (Season 4) also corresponds to the period of the outflow current flowed along the southern part of the bay. The results suggest that the distribution and abundance of colonial ascidians in Otsuchi Bay probably correlate with the outflow of water current in the bay.

Differences in the amount of sessile organisms between the depths

Distribution of sessile organisms in Otsuchi Bay showed different depth patterns depending on the species. Barnacles M. rosa and B. trigonus showed clear differences in depth patterns in Season 1. Megabalanus rosa tended to be abundant at 5-10m deep in Otsuchi Bay, and this tendency was also reported in a previous report at another locality in Japanese waters (Ito and Kajihara 1988). Various environmental factors such as temperature and salinity were reported as the factors determining the settlement of barnacle larvae (Crisp 1955, Crisp and Ritz 1973, Kon-ya and Miki 1994, Nogata et al. 2011). Although salinities were measured only four times in the present study, no significant differences in temperature and salinity were detected between the depths observed at each locality. Therefore, the settlement of barnacles in Otsuchi Bay is determined by not only temperature and salinity, but also by other factors probably affected by their depth distributions. Light intensity has been previously reported as one of the factors determining the settlement patterns of barnacles (Barnes et al. 1951, Forbes et al. 1971). In the present study, we detected large differences in light intensity between the depths, and therefore, the depth distribution patterns of barnacles in Otsuchi Bay are considered to be related to the light intensity. As Balanus trigonus was particularly abundant at deeper depths and the lower-surface of the panels, this species may prefer to settle or grow well in the shade of mooring structures and/or deeper depths. Barnacles were not common on the panels at Station 1, and thus the locality of Station 1 may not be suitable for some barnacle species. *Megabalanus rosa* was also not common at Stations 1 and 4 in the inner part of the bay, and tended to be particularly abundant at the entrance of the bay, which corresponds to the results of previous studies conducted at several other localities in Japan as reviewed in Horikoshi and Okamoto (2007).

Growth rates (estimated from dry weight of individuals) of barnacles tended to increase with decreasing the depth. The growth rates of barnacles on settlement panels probably not only depend on the richness of food resources, but also strongly restricted depending on their density.

The amount of bryozoan colonies at shallower depths at Station 4 was remarkably larger than any other localities in Season 2 (Figs. 15 and 16). The fluorescent values at shallower depths at Station 4 were remarkably high in November and February (Fig. 4); therefore, the large amount of bryozoan colonies at Station 4 might be due to the rapid growth of colonies with the enough food resources at shallower depths. Larvae of gymnolaemate bryozoans generally display positive phototaxis (Mawatari 1951a, 1951b, 1952, Ryland 1960, 1977); therefore, the behavior of the larvae also probably caused the shallower distribution of bryozoan colonies on the settlement panels.

In the present study, the area of colonial ascidians including *Didemnum* sp. tended to be abundant in 5–10 m deep, and also slightly more abundant on the lower-surface of the panels. The larvae of some colonial ascidians (*Diplosoma* and *Didemnum*) generally display positive phototaxis during early stages, subsequently they display negative phototaxis and negative geotaxis, and the settlement is abundant on shaded lower-surface where the survival is highest (Hurlbut 1993). Although the depth distribution is not only determined by larval behavior (Crisp and Ghobashy 1971, Hurlbut 1991), the distributions of colonial ascidians in Otsuchi Bay were consistent with the reported behavior of the larvae.

Solitary ascidians *C. savignyi* and *C. japonica* were remarkably abundant at Station 1 located in the inner part of the bay. Solitary ascidian *Ascidiella aspersa* (Muller, 1776) is well known as an organism causing serious fouling problems on cultured scallops on the Sanriku Coast (Chida et al. 2011), however this species was not found in Otsuchi Bay in this study. Although the number of solitary ascidians was largely different between the panels, the concentrated attachment on lower-surface of the panels may cause various fouling problems at shade of mooring objects in aquaculture facilities.

Succession pattern of sessile organisms on settlement panels in Otsuchi Bay

Bryozoan diversity on settlement panels was highest in Season 1, from August to November (Fig. 13). Bryozoans in temperate areas in Sweden and Norway generally have a peak of breeding during summer and autumn (Ryland 1963, 1970, Ström 1977). The results in the present study indicate that most fouling bryozoan species in Otsuchi Bay have similar breeding seasons as well as other temperate bryozoans, and the highest bryozoan diversity during summer and autumn is due to the breeding season. *Pacificincola* sp. bears numerous ovicells with embryos inside in summer (Fig. 7C). Subsequently, most of the ovicells were found as being empty in autumn (Fig. 7A). These results indicate the release of the larvae during autumn.

On the other hand, species composition of bryozoans in Season 4 was different from the other seasons; some coldwater species such as *Callopora* sp. and *Celleporella* sp. tended to be abundant. Season 4 started in the coldest season (the end of April) in Otsuchi Bay (Fig. 2); therefore, the abundance of cold-water species in this season indicates that these species have a peak of breeding in coldest early spring in Otsuchi Bay. The remarkable decrease of sessile organisms in Season 3 (from February until April) was probably due to the lower temperature and the increase of macroalgae on the upper-surface of the panels.

At the end of August, barnacles were not found on the settlement panels in the observation three weeks after being submerged. The time-lag of barnacle settlement corresponds to the results of a previous study in Otsuchi Bay (Kado et al. 1980). The settlement of barnacles is also affected by bacterial biofilms and some hormones produced by the adult barnacles (Wieczorek and Todd 1998, Crisp and Meadows 1962, 1963). Although it is not able to determine the factor of the time-lag in the present study, this result suggests that some kind of chemical and physical factors need to be prepared on settlement panels to get barnacle settles.

The interspecific competition among sessile organisms is an important factor in the succession of sessile organism assemblage (Osman 1977, Hirata 1987). In contrast, the complexity of physical aspects of algal structure is an important factor producing the increasing diversity and abundance of associated invertebrates in the early and middle stages of algal succession (Dean and Connell 1987a, b). In the present study, both interspecific competition and the complexity of physical aspects of sessile organisms were supposed to be important factors in the succession of sessile organism assemblage on mooring settlement panels in Otsuchi Bay. The succession of sessile organisms on settlement panels in Otsuchi Bay is supposed to be started with colonial organisms (Fig. 17). On the panels deployed in summer, a number of hydroids and some colonial ascidians were observed on the panels three weeks after deployment. Hydroids, colonial ascidians and bryozoans were obtained throughout the year; therefore, these colonial organisms are considered to be a primary colonizer on new substrates in early successional stages in Otsuchi Bay. Other solitary organisms, such as barnacles and mussels, are supposed to be a secondary colonizer, which made complexity of physical aspects increase on the surface of substrates (Fig. 17); they provide a suitable substrate to small bivalves (e.g., Musculus cf. nipponicus), polychaetes and some solitary ascidians (e.g., S. clava) in the middle successional stages. Scheer (1945) reported a similar succession pattern that bryozoans were followed by Styela or Mytilus in Newport Harbor, California. Furthermore, the succession pattern of sessile organisms in Nabeta Bay in Izu Peninsula (Hirata 1987) was also similar to the succession in Otsuchi Bay, except the barnacles were obtained as the "earliest colonizer" in Nabeta Bay. In the present study, the surface of panels and settled organisms such as barnacles and bryozoans were often completely covered by the colonial ascidians in the later successional stages. This causes death of the covered sessile organisms, and the shells of dead organisms may also provide the substrates to new recruitments after the colonial ascidians disappeared (Fig. 17). The results indicate the importance of competition in later stages of the succession of sessile organism assemblages.

The present study revealed the diversity and seasonal changes in sessile organism assemblages on mooring substrates in Otsuchi Bay, based on observations over a single year. The results on species composition and distribution of the sessile organisms will largely contribute to predict the appearing taxa on cultured bivalves at different depths and areas in the bay (e.g., shallow distribution of barnacle species *M. rosa*). Although it shows the succession within an year, the results on seasonality and growth rate of sessile organisms with environmental data enable us to determine the appropriate season for preventing these fouling organisms (e.g., barnacles and bryozoans in summer, and colonial ascidians in early spring). In this study, the longest submerged period of settlement panels was six months (two seasons). Many aquaculture facilities are generally deployed more than an year; therefore, the further survey using settlement panels deployed throughout an year will provide information on the succession of sessile organisms on culturing facilities in more detail.

Sessile organisms are also known as potential competitors to cultured oysters and scallops. The results of the present study, therefore, also provide basic information on the amount of potential consumers of natural food resources in the bay, to estimate the appropriate amount of cultured bivalves to maintain sufficient food resources. The culturing facilities have been already started to be restored after the earthquake and tsunami in Otsuchi Bay. The amount of sessile organisms in the bay might be changed by the increase of the aquacultured competitors and floating substrates, and the amount and composition of sessile organisms in the bay may change according to the restoration of the aquaculture fisheries in the bay. It is necessary to continue to monitor the changes in sessile organism assemblages in the bay to observe the changes of the amount and species composition according to the restoration and to detect the serious fouling problem at an early stage.

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References

- Barnes, H., Crisp, D. J. and Powell, H. T. 1951. Observations on the orientation of some species of barnacles. J. Anim. Ecol. 20: 227–241.
- Chida, K., Onodera, T. and Haga, K. 2011. Notes on the identification of invaded European sea squirt *Ascidiella aspersa* along Miyagi coasts. Miyagi Pref. Rep. Fish. Sci. 11: 79–81.
- Crisp, D. J. 1955. The behavior of barnacle cypris in relation to water movement over a surface. J. Exp. Biol. 32: 569–590.
- Crisp, D. J. and Ghobashy, A. F. A. A. 1971. Responses of the larvae of *Diplosoma listerianum* to light and gravity. In: Crisp, D. J. (ed.), Proceedings of the 4th European Marine Biology Symposium, pp. 443–465, Cambridge University Press, Cambridge, UK.
- Crisp, D. J. and Meadows, P. S. 1962. The chemical basis of gregariousness in cirripedes. P. Roy. Soc. Lond. B Bio. 156: 500–520.
- Crisp, D. J. and Meadows, P. S. 1963. Absorbed layers: the stimulus to settlement in barnacles. P. Roy. Soc. Lond. B Bio. 158: 364– 387.
- Crisp, D. J. and Ritz, D. A. 1973. Responses of cirripede larvae to light. I. Experiments with white light. Mar. Biol. 23: 327–335.
- Dean, R. L. and Connel, J. H. 1987a. Marine invertebrates in an algal succession. I. Variations in abundance and diversity with succession. J. Exp. Mar. Biol. Ecol. 109: 195–215.
- Dean, R. L. and Connel, J. H. 1987b. Marine invertebrates in an algal succession. II. Tests of hypotheses to explain changes in diversity with succession. J. Exp. Mar. Biol. Ecol. 109: 217– 247.
- Dziubińska, A. and Janas, U. 2007. Submerged objects-a nice place to live and develop. Succession of fouling communities in the Gulf of Gdańsk, Southern Baltic. Oceanol. Hydrobiol. St. 36: 65–78.
- Forbes, L., Seward, M. J. B. and Crisp, D. J. 1971. Orientation to light and the shading response in barnacles. In: Crisp, D. J. (ed.), Proceedings of the 4th European Marine Biology Symposium, pp. 539–558, Cambridge University Press, Cambridge, UK.
- Glasby, T. M. 1998. Estimating spatial variability in developing assemblages of epibiota on subtidal hard substrata. Mar. Freshwater Res. 49: 429–437.
- Glasby, T. M. 2001. Development of sessile marine assemblages on fixed versus moving substrata. Mar. Ecol-Prog. Ser. 215: 37-

47.

- Glasby, T. M. and Connell, S. D. 2001. Orientation and position of a substratum have large effects on epibiotic assemblages. Mar. Ecol-Prog. Ser. 214: 127–135.
- Hirata, T. 1986. Succession of sessile organisms on experimental plates immersed in Nabeta Bay, Izu Peninsula, Japan. I. Algal succession. Mar. Ecol-Prog. Ser. 34: 51–61.
- Hirata, T. 1987. Succession of sessile organisms on experimental plates immersed in Nabeta Bay, Izu Peninsula, Japan. II. Succession of invertebrates. Mar. Ecol-Prog. Ser. 38: 25–35.
- Hirata, T. 1991. Succession of sessile organisms on experimental plates immersed in Nabeta Bay, Izu Peninsula, Japan. III. Temporal Changes in Community Structure. Ecol. Res. 6: 101–111.
- Horikoshi, A. and Okamoto, K. 2007. Present structure of sessile organism communities on lighted buoys in Tokyo Bay. Sessile Organisms 24: 21–32.
- Hurlbut, C. J. 1991. The effects of larval abundance, settlement and juvenile mortality on the depth distribution of a colonial ascidian. J. Exp. Mar. Biol. Ecol. 150: 183–202.
- Hurlbut, C. J. 1993. The adaptive value of larval behavior of a colonial ascidian. Mar. Biol. 115: 253–262.
- Ishizu, M., Itoh, S., Tanaka, K. and Komatsu, K. 2016. Mooring observations of ocean circulation in Otsuchi Bay, Japan influenced by open ocean conditions. In: Kogure, K., Hirose, M., Kitazato, H. and Kijima, A. (eds.), Marine ecosystems after Great East Japan Earthquake in 2011. Our knowledge acquired by TEAMS. pp. 37–38. Tokai University Press, Kanagawa.
- Ito, N. and Kajihara, T. 1988. Ecological studies of a large barnacle, *Megabalanus rosa* I Settlement, growth, mortality and vertical distribution on the observation tower off Hiratsuka in Sagami Bay. Marine Fouling 7: 31–40. (in Japanese)
- Kado, R., Hino, A. and Hirano, R. 1980. Barnacles (Cirripedia, Thoracica) in Otsuchi Bay, breeding and settling seasons of boreoarctic and warm water species. Otsuchi Marine Research Center Report 6: 7–12. (in Japanese)
- Kajihara, T. and Ura, Y. 1976. Sessile organisms in Otsuchi Bay. Otsuchi Marine Research Center Report 2: 20–29. (in Japanese)
- Kon-ya, K. and Miki, W. 1994. Effects of environmental factors on larval settlement of the barnacle *Balanus amphitrite* reared in the laboratory. Fisheries Sci. 60: 563–565.
- Mawatari, S. 1951a. The natural history of a common fouling bryozoan, *Bugula neritina* (Linnaeus). Miscellaneous Reports of

the Research Institute for Natural Resources (Tokyo) 20: 47– 54.

- Mawatari, S. 1951b. On *Tricellaria occidentalis* (Trask), one of the fouling bryozoans in Japan. Miscellaneous Reports of the Research Institute for Natural Resources (Tokyo) 22: 9–16.
- Mawatari, S. 1952. On *Watersipora cucullata* (Busk). II. Miscellaneous Reports of the Research Institute for Natural Resources (Tokyo) 28: 17–27.
- Nogata, Y., Tokikuni, N., Yoshimura, E., Sato, K., Endo, N., Matsumura, K. and Sugita, H. 2011. Salinity limitations on larval settlement of four barnacle species. Sessile Organisms 28: 47–54. (in Japanese)
- Osman, R. W. 1977. The establishment and development of a marine epifauna community. Ecol. Monogr. 47: 37–63.
- Otobe, H., Onishi, H., Inada, M., Michida, Y. and Terazaki, M. 2009. Estimation of water circulation in Otsuchi Bay, Japan inferred from ADCP observation. Coastal Marine Science 33: 1–9.
- R Development Core Team (2011) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria http://www.R-project.org
- Ryland, J. S. 1960. Experiments on the influence of light on the behavior of polyzoan larvae. J. Exp. Biol. 37: 783–800.
- Ryland, J. S. 1963. Systematic and biological studies on Polyzoa (Bryozoa) from western Norway. Sarsia 14: 1–60.
- Ryland, J. S. 1970. Bryozoans. pp. 175, Hutchinson University Library, London.
- Ryland, J. S. 1977. Taxes and tropisms of bryozoans. In: Woollacott, R. M. and Zimmer, R. L. (eds.), Biology of Bryozoans, pp. 411–436, Academic Press, New York.
- Scheer, B. T. 1945. The development of marine fouling communities. Biol. Bull. 89: 102–121.
- Ström, R. 1977. Brooding patterns of bryozoans. In: Woollacott, R. M. and Zimmer, R. L. (eds.), Biology of Bryozoans, pp. 23–55, Academic Press, New York.
- Wieczorek, S. K. and Todd, C. D. 1998. Inhibition and facilitation of settlement of epifaunal marine invertebrate larvae by microbial biofilm cues. Biofouling 12: 81–118.
- Yamaguchi, T. 1977. Taxonomic studies on some fossil and recent Japanese Balanoidea (Part 2). Trans. Proc. Palaeont. Soc. Japan 108: 161–201.