Coastal Marine Science 40(2): 55–65, 2017

Temporal changes in the surf zone fish assemblage in Otsuchi Bay, Pacific coast of northeastern Japan, with comments on influences of the 2011 Tohoku earthquake and tsunami

Tomoaki GOTO[1]*, Airi TAKANASHI[2], Satoru TAMADA[3] and Ken-ichi HAYASHIZAKI[3]

[1] *Sanriku Fisheries Research Center, Iwate University, Heita, Kamaishi, Iwate 026–0001, Japan*
[2] *Iwate Fisheries Technology Center, Heita, Kamaishi, Iwate 026–0001, Japan*
[3] *Laboratory of Aquatic Animal Ecology, Kitasato University School of Marine Biosciences, Kitasato, Minami Ward, Sagamihara, Kanagawa 252–0373, Japan*
* *E-mail: tgoto@iwate-u.ac.jp*

Received 1 May 2016; Accepted 9 October 2016

Abstract— Effects of the 2011 Tohoku earthquake and tsunami on the surf zone fish assemblage during summer to autumn in Otsuchi Bay, Pacific coast of northeastern Japan, were evaluated based on the species composition and abundances of 46 fish species collected by bottom towing surveys from 2009 to 2015. The fish community was characterized by the juveniles of epibenthic species preferring bare sandy habitat, viz. *Upeneus japonicus*, *Repomucenus curvicornis*, *R. lunatus*, *Paralichthys olivaceus*, *Tarphops oligolepis* and *Pleuronectes yokohamae*, and the species associated with seagrass or macroalgal habitat, viz. *Pholis crassispina*, *P. nebulosa* and *Rudarius ercodes*, according to SIMPER analysis. While no significant differences were found in the physical water condition, total abundance, or species diversity and richness indices, cluster and canonical correspondence analyses showed that the post-earthquake species composition was clearly distinct from the pre-earthquake communities by the increase of demersal fish species associated with sandy substrate, such as *Favonigobius gymnauchen* and flatfishes, in contrast to the reduction of seagrass or macroalgal dependent fish species. The results suggest that the disturbance of tsunami has affected the expansion of the nursery and/or feeding potential for epibenthic species, including many commercial pleuronectid flatfishes, caused by the replacement of substratum by sandy sediment.

Key words: Cluster, CCA, surf zone, fish fauna, habitat

Introduction

Surf zones are shallow waters formed off sandy beaches, with a continuous physical flux created by tides and waves (McLachlan and Brown 2006). Although surf zone fish faunas have been characterized as structurally homogeneous, a number of studies have found that fluctuations in physical variables (wave height, turbidity, sand grain size, beach slope, temperature and salinity) and temporal scales (seasons, tidal level, moon stage and time of day) can alter the composition and species richness of the faunal assemblages (e.g., Watkin 1941, Colman and Segrove 1955, Hamerlynck and Mees 1991, Clark et al. 1996, Lock et al. 1999, Beyst et al. 2001, Dominguez Granda et al. 2004, McLachlan and Brown 2006, Inui et al. 2010). Recently, it has been suggested that surf zones play multiple roles, including functioning as transit routes and/or habitats for many fish species (McLachlan and Brown 2006). The most distinctive features of such communities are their great variability in space and time, their opportunistic feeding behavior, and the high proportion of larvae and juveniles (Senta and Kinoshita 1985, McLachlan and Brown 2006, Félix et al. 2007, Able et al. 2013). In surf zone fish communities, seasonal fluctuations in physical conditions, including wave action and temperature, and anthropogenic disturbances affect both larval and juvenile assemblages (Machado Pessanha and Araújo 2003, McLachlan and Brown 2006, Inui et al. 2010, Pereira et al. 2013). Thus, drastic changes caused by environmental factors, such as tsunami and heavy rain, impact directly on fish assemblages characterized by passive migration stages.

The Sanriku area, northeastern Japan, is characterized by a ria coast having many narrow bays facing the Kuroshio–Oyashio mixture waters of the northwestern Pacific. This region was damaged heavily by a massive tsunami triggered by the Tohoku earthquake (magnitude 9.0) on March 11, 2011. The narrow bays focused the tsunami waves, generating the largest inundation heights and run-ups (Mori et al. 2011). Otsuchi Bay, located at the middle of the ria coastline, was one of the areas damaged heavily by the tsunami, waves reaching more than 17 m in height (Mori et al. 2011). At Nebama, at the southern estuary of the Unosumai River facing the innermost part of the bay, the tsunami eroded most of the material comprising a sandy beach and sandbar, such conditions remaining still (Okayasu et al. 2013). Several meters depth of seabed sediments were eroded by the tsunami in water depths of 10–20 m along the ria coast, the subtidal seafloor ecosystem being seriously affected (Goto et al. 2012). In Otsuchi Bay, the impact of the tsunami on macrobenthos distribution varied by species, depending upon the environmental conditions (Seike et al. 2013).

Prior to the 2011 earthquake and tsunami, many coastal fish species preferring either cold or warm waters had been recorded in Otsuchi Bay (Iwata and Numachi 1981, Tatsukawa and Tanaka 1982, Takahashi et al. 1999). The innermost area of the bay was known to have a nursery function for various coastal fishes, including commercially important species such as Japanese flounder, *Paralichthys olivaceus*, sand lance, *Ammodytes personatus*, marbled sole, *Pleuronectes yokohamae*, Japanese surf smelt, *Hypomesus pretiosus japonicus*, chum salmon, *Oncorhynchus keta* and ayu, *Plecoglossus altivelis altivelis* (Hirose and Kawaguchi 1997, Takahashi et al. 1999, Yamashita and Aoyama 1984, Goto 2014, 2015). In the Sanriku area, the number of coastal species increased in the spring season from March to May (Yamashita and Aoyama 1984, Kawabata 1997). However, the March 2011 tsunami impacted directly on the habitat of these juvenile fishes, the subsequent habitat changes, such as lost of the sandbar, possibly influencing long-term future recruitment.

In this study, seasonal and annual fluctuations in surf zone fish assemblages in Otsuchi Bay during summer to autumn were determined following bottom towing surveys conducted from 2009 to 2015. Influences of the 2011 Tohoku earthquake and tsunami were also evaluated.

Materials and Methods

1. Study area

The present study was conducted in the surf zone off Nebama, located at the innermost part of Otsuchi Bay, Pacific coast of northeastern Japan (Fig. 1). The study area was characterized by shallow water, up to 10 m in depth, adjacent to the Unosumai River estuary and seagrass beds (Komatsu et al. 2003). Although formerly well distant from the river mouth (800 m) due to a sandbar, that distance is now much shortened following the erosion of the sandbar by the 2011 tsunami (Okayasu et al. 2013).

2. Sampling

In this study, the abundance and diversity of fishes were assessed from bottom towing surveys carried out by the fishing vessel for set-net, Horai-maru, Kobayashi Set-net Fisheries Cooperative and R/V Grand Maillet, International Coastal Research Center, Atmosphere and Ocean Research Institute (AORI), from 2009 to 2010 and from 2011 to 2015, respectively. Samples were collected in early and late August, September, and October to early November for each year, using a sledge net with a 200×20 cm stainless frame, a tickler chain and 4 mm mesh size of the cod net. Two or three sets of towing runs at 2–3 knots for 2–3 minutes on the seafloor were conducted at three depth strata (5–6 m, 7–8 m and 9–10 m) from 8:00 to 12:00 to reduce any bias caused by daily distributional shifts or migration, in each survey. At each station, water temperature and salinity were recorded from the sea surface to the bottom using a compact CTD (Alec co ltd.). The towing distance was measured by a compact GPS track-

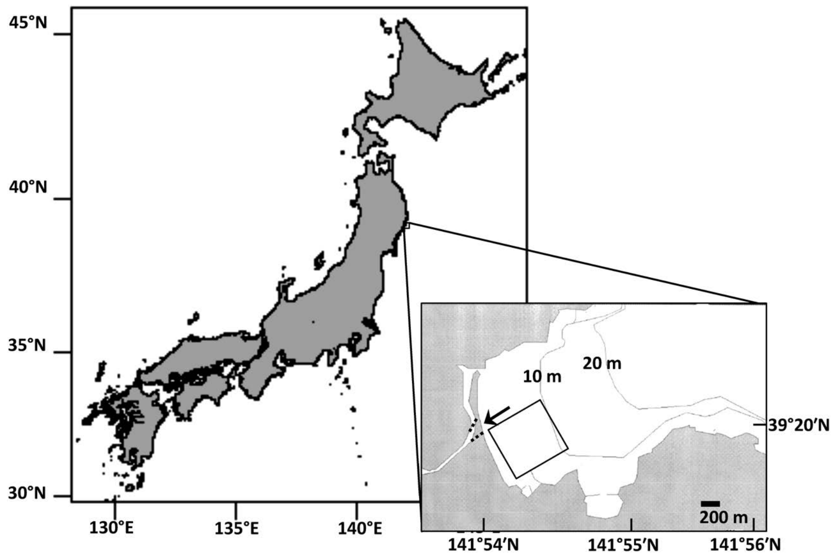

Fig. 1. Map of the innermost area of Otsuchi Bay, showing the study area (enclosed by square). Dotted lines and arrow indicate current river flow and mouth, respectively.

ing device (GARMIN co ltd.). Fish collected were preserved in 85% ethanol on board, and identified to species level, counted and measured (total length: TL) to the nearest millimeter in the laboratory.

3. Data analysis

Fish abundance was defined as mean numbers of individuals per 1000 m^2 in each survey, mean temperature and salinity at 5 m depth at all stations being used as environmental parameters for the data analyses. The environmental parameters were tested among years and between pre- and post-earthquake periods, using one-way analysis of variance (ANOVA) and Mann–Whitney *U* test, respectively. For the data analyses, the taxonomic unit was set at species level. Due to the study area being known as a settlement and nursery area of Japanese flounder, *P. olivaceus*, one of the dominant species in Otsuchi Bay (Goto 2007, 2014), the operational unit for that species was divided into newly settled 0 year-old juvenile (0 y-o) and one year-old or over (≥ 1 y-o), representing different trophic levels (characterized by ontogenetic habitat shift with change of prey items from crustaceans dominated by mysids to fish, such as *Engraulis japonicus*, during summer to autumn) (Yamada et al. 1998, Yamaguchi et al. 2007, Tomiyama et al. 2011). In Iwate Prefecture, a total of more than a million hatchery-reared juveniles of Japanese flounder and barfin flounder, *Verasper moseri*, were released annually as a stock enhancement program until 2010 (Sasaki and Nakai 2006, Goto 2007). Most of the reared flatfish are recognized mainly by having abnormal pigmentations on the blind side (Tomiyama et al. 2008, Wada et al. 2013). In this study, the 0 year-old juveniles with such pigmentations were excluded from the data sets for both species.

Species diversity was assessed using the Shannon-Wiener index (Shannon and Weaver 1963):

$$H' = -\sum_{i=1}^{S} p_i \ln p_i,$$

where S and P_i are the total number of species and relative frequency of species in each survey, respectively. Species richness was shown as the number of species in each survey.

Temporal changes of the fish assemblages were assessed between seasons and years by cluster analysis using the Bray–Curtis similarity coefficient. The distance was calculated by applying Ward's method to form hierarchical clusters. Before the analysis, fish species occurring in only one survey were excluded. Abundance data were transformed to the corresponding $\log_{10}$ (x+1). Groups found on the cluster were tested using analysis of similarity (ANOSIM) statistics (Clarke 1993, Clarke et al. 2008).

Similarity percentages (SIMPER: Clarke 1993) were used to determine which species were most responsible for the Bray–Curtis dissimilarity between groups. Indicator values were calculated for all species examined in order to identify indicator species in sample groups derived from the cluster analysis (Dufrêne and Legendre 1997). When the indicator value was maximal for a species across groups of stations, that species was considered as an indicator species for that assemblage and group of stations. Species with a maximum indicator value greater than 15% were defined as "key species" of an assemblage (Chouinard and Dutil 2011). The canonical correspondence analysis (CCA) was used for the evaluation of the variability in assemblage structure in relation to the selected factors from temporal (month and pre- and post-earthquake periods) and hydrological (temperature and salinity) parameters. The temporal and environmental variables were tested using a Monte Carlo test with permutations (1000 permutations, a=0.05; Ter Braak 1986). Indices of diversity and species richness were tested using Welch's *t* test and Kruskal–Wallis test between pre- and post-earthquake periods and among the groups from the cluster analysis, respectively. All multivariate analyses were performed using the vegan package (Oksanen et al. 2013) in statistical software R (R Development Core Team 2008) or the PAST software (Hammer et al. 2001).

Results

1. Environmental parameters

Mean temperature and salinity at 5 m depth varied seasonally, ranging from 19.1–22.1°C and 33.0–33.5 (2009); 17.6–23.1°C and 33.4–33.6 (2010); 20.8 and 32.7 (2011); 18.9–21.0°C and 33.6–33.8 (2012); 18.6–22.0°C and 32.3–33.5 (2013); 18.8–20.7°C and 33.1–33.5 (2014); 18.5–19.2°C and 33.4–33.8 (2015), respectively (Fig. 2). No consistent trends were present, although significant differences were found in both temperature (Temp.) and salinity (Sal.) among the years for three periods available to compare statistically, i.e., early (Temp.: F=87.3, p<0.001; Sal.: F=139.6, p<0.001) and late (Temp.: F=543.2, p<0.001; Sal.: F=178.5, p<0.001) August, and September (Temp.: F=16765.0, p<0.001; Sal.: F=1805.2, p<0.001). A comparison between pre- and post-earthquake periods found no significant differences in either parameter (Temp.: U=779.9, p=0.37; Sal.: U=779.7, p=0.22).

2. Fish abundance and composition

A total of 46 species belonging to 27 families (except hatchery-reared fishes) were collected from the study area throughout the study period from 2009 to 2015 (Table 1). Pleuronectidae and Callinymidae dominated species numbers, despite varying annually in each survey from 12 to 16 in 2009 (early August–September), from 7 to 17 in 2010 (early August–November), 13 in 2011 (September), from 10 to 17 in 2012 (early August–October), from 11 to 14 in 2013 (early August–October), from 8 to 16 in 2014 (early August–

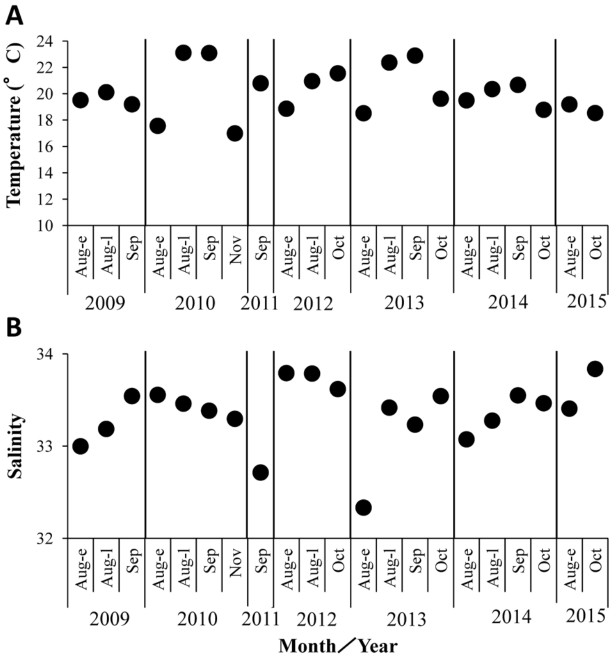

Fig. 2. Fluctuations in mean water temperature (A) and salinity (B) of 21 surveys from 2009 to 2015. Abbreviations "e" and "l" following month indicate early and late, respectively.

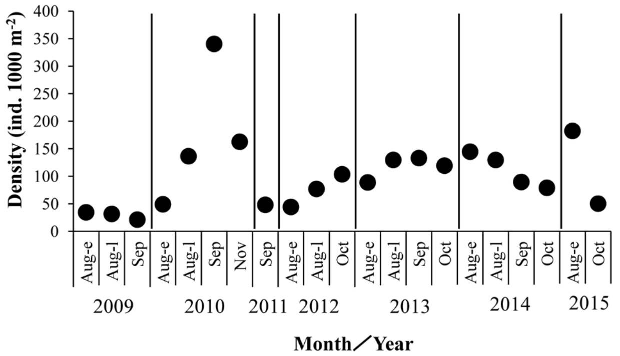

Fig. 3. Fluctuations in total density (ind. $1000\,m^{-2}$) of 21 surveys from 2009 to 2015. Abbreviations "e" and "l" following month indicate early and late, respectively.

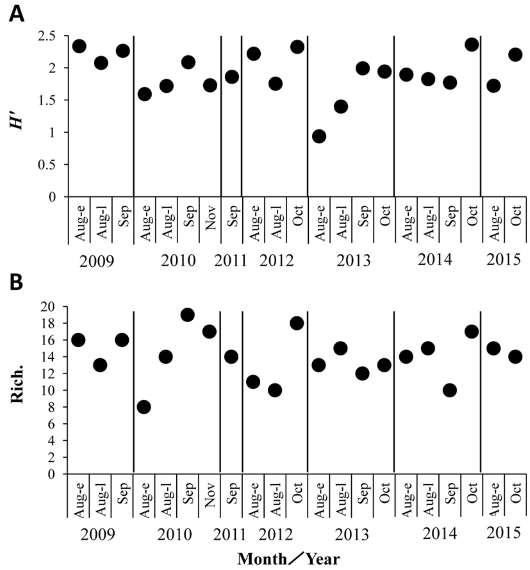

Fig. 4. Fluctuations in species diversity index (H') and species richness (Rich.) for 21 surveys from 2009 to 2015. Abbreviations "e" and "l" following month indicate early and late, respectively.

October) and 12 or 13 in 2015 (early August–October). The sampling season with the highest number of species differed among years, i.e., early August (2009 and 2015), late August (2013), September (2010) and October (2012 and 2014).

The total density of all species varied greatly from 21.3 ind. $1000\,m^{-2}$ to 340.4 ind. $1000\,m^{-2}$ (mean 105.8 ind. $1000\,m^{-2}$), as shown in Fig. 3. No consistent patterns in range or seasonal trend were apparent among years: 21.3 (September)–42.6 (early August) ind. $1000\,m^{-2}$ in 2009; 49.1 (early August)–340.4 (September) ind. $1000\,m^{-2}$ in 2010; 50.4 (September) ind. $1000\,m^{-2}$ in 2011; 44.3 (early August)–103.6 (October) ind. $1000\,m^{-2}$ in 2012; 88.8 (early August)–133.1 (September) ind. $1000\,m^{-2}$ in 2013; 80.0 (October)–154.5 (early August) ind. $1000\,m^{-2}$ in 2014; 50.3 (October)–182.4 (early August) ind. $1000\,m^{-2}$ in 2015. A comparison between the pre- and post-earthquake periods found no significant difference in total density (Welch's t test: t=0.21, p=0.84).

The dominant families, based on individual densities, included Callinymidae, Mullidae, Paralichthyidae and Pleuronectidae in most case, ranging from 29.7–93.8% (mean: 71.8%). The species diversity index (H') and species richness (Rich.) ranged between 0.94 and 2.36 (mean 1.91), and 0.19 and 0.44 (mean 0.34), respectively (Table 1; Fig. 4). Seasonal changes in both indices differed among study years, although no significant differences were found between pre- and post-earth quake periods (Welch's t test: H' t=0.55, p=0.82; Rich. t=0.89, p=0.40). The total number of species increased from 30 to 39 after 2011, including 23 species (50.0% of all species encountered during the study) collected in both periods (Table 1). The number of species collected only from one or other period changed from seven to 16, including six pleuronectid flatfishes (Table 1).

Hierarchical cluster analysis classified the summer and autumn surveys conducted from 2009 to 2015 into three groups (A–C) at dissimilarity 1.0, based on Bray–Curtis similarity of fish abundances over a total of 21 surveys (Fig. 5). The analysis of similarity (ANOSIM) showed significant dissimilarity among the groups (r=0.77, p<0.001). They were summarized as ten surveys during September to November except for late August in 2010 (group A), four in early to late August in the pre-earthquake years (including September in 2009) (group B), and seven conducted in August in the post-earthquake years (group C). No significant differences were found in H' or species richness among the groups (Kruskal–Wallis test: H' Chi^2=3.61, p=0.16; Rich. Chi^2=1.25, p=0.53).

Table 1. Results of 21 surveys conducted in surf zone of Otsuchi Bay from 2009 to 2015, showing indices of H', mean total length and mean density (ind. $1000\,m^{-2}$) by species. Abbreviations e and l shown with survey month indicate early and late, respectively.

Family	Species	Mean TL (mm)	Mean density (ind. $1000\,m^{-2}$)																				
			2009			2010				2011	2012			2013				2014				2015	
			e-Aug	l-Aug	Sep	e-Aug	l-Aug	Sep	Nov	Sep	e-Aug	l-Aug	Oct	e-Aug	l-Aug	Sep	Oct	e-Aug	l-Aug	Sep	Oct	e-Aug	Oct
H'			2.34	2.08	2.26	1.59	1.72	2.09	1.73	1.86	2.22	1.75	2.33	0.94	1.40	1.99	1.94	1.89	1.82	1.77	2.36	1.72	2.20
Rajidae	*Okamejei kenojei*	155.1	1.5	0.0	0.0	1.3	0.8	2.8	1.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0
Congridae	*Conger myriaster*	300.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Engraulidae	*Engraulis japonicus*	54.8	0.0	0.0	0.5	0.0	0.0	0.0	0.0	15.4	0.0	0.0	19.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.0	0.0	5.4
Zeidae	*Zeus faber*	32.2	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Syngnathidae	*Hippocampus mohnikei*	55.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.8	1.5	2.1	0.0	0.0	0.0	0.0	0.0	0.0
	Syngnathus schlegeli	128.8	0.0	0.5	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sebastidae	*Sebastes cheni*	50.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Sebastes schlegeli	45.6	0.7	0.5	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	12.4	0.0	0.0	0.0	0.0	0.0
Tetrarogidae	*Hypodytes rubripinnis*	25.3	0.0	0.0	0.0	0.0	0.0	15.4	5.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Triglidae	*Chelidonichthys spinosus*	42.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.6	9.4	0.0	2.9	0.0	0.0	1.7	0.0	0.0	0.0	1.0	4.7	0.0
	Lepidotrigla microptera	46.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.0	0.0	0.0	0.0	1.4	0.0	0.0	0.0	0.0
Platycephalidae	*Suggrundus meerdervoortii*	72.1	0.0	0.0	0.0	0.0	0.0	3.1	0.0	0.0	0.0	0.0	2.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mullidae	*Upeneus japonicus*	53.1	6.4	5.9	3.7	7.8	34.5	39.0	7.4	15.4	3.5	18.5	13.6	2.1	10.5	11.9	6.8	45.3	32.4	27.3	0.0	6.5	1.1
Sparidae	*Pagrus major*	35.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.0	1.0	0.0	0.8	0.0	0.0	0.0	1.4	0.0	0.0	3.5	0.0
Carangidae	*Trachiurus japonicus*	31.2	8.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sillagonidae	*Sillago japonica*	36.1	0.0	0.0	0.0	0.0	0.0	0.0	1.3	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Agonidae	*Occella iburia*	87.7	4.1	2.1	0.5	0.0	1.6	0.0	0.0	0.0	3.0	0.7	0.0	0.0	0.0	0.0	0.0	3.4	2.1	0.0	0.0	0.0	0.0
Hexagrammiidae	*Hexagrammos otakii*	154.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cottidae	*Furcina ishikawae*	37.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.4	0.0	0.0	0.0	0.0
	Gymnocanthus intermedius	59.9	0.7	0.0	0.0	6.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8.3	11.1	0.0	0.0	12.3	0.0
	Pseudoblennius cottoides	64.3	1.5	0.0	1.0	0.0	1.2	0.0	0.0	0.0	5.2	0.0	0.0	2.0	0.8	2.1	1.3	2.3	0.0	0.0	0.0	3.5	0.0
Hemitripteridae	*Blepsias cirrhosus*	116.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0
Liparidae	*Liparis agassizii*	147.0	0.0	1.1	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Callinymidae	*Repomucenus beniteguri*	80.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.1	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.4	2.1	2.2
	Repomucenus curvicornis	50.4	0.0	0.0	0.0	0.0	50.4	63.3	0.0	1.8	2.4	0.0	3.6	0.0	0.0	19.4	28.9	0.0	0.0	0.0	22.4	0.0	0.0
	Repomucenus lunatus	47.1	0.0	0.0	0.0	0.0	0.0	22.7	49.2	1.2	0.0	0.0	0.0	1.1	0.0	8.5	19.9	1.1	0.0	1.0	4.4	0.0	6.7
	Repomucenus ornatipinnis	146.5	0.0	0.0	0.0	0.0	0.0	1.3	0.0	0.0	6.9	0.0	1.6	0.9	0.0	0.0	2.1	3.4	1.4	0.0	1.6	4.4	1.0
	Repomucenus valenciennei	50.3	0.0	0.0	2.7	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	25.5	6.7	0.0	0.0
Gobiidae	*Favonigobius gymnauchen*	58.0	1.1	2.1	0.0	0.0	0.7	0.0	0.0	1.4	0.0	0.0	0.0	1.1	1.6	2.2	0.0	5.7	8.8	7.6	8.5	1.2	2.1
Pholidae	*Pholis crassispina*	73.9	7.4	5.2	0.9	4.2	0.0	3.3	3.3	1.8	2.3	11.3	0.0	1.1	0.0	0.0	0.0	4.6	1.4	0.0	4.5	0.0	0.0
	Pholis nebulosa	127.4	3.4	8.4	4.1	6.8	0.7	0.8	1.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Paralichthyidae	0 y-o *Paralichthys olivaceus*	60.4	2.2	2.1	1.0	1.3	14.4	11.5	6.2	1.7	3.8	19.2	11.1	5.0	34.8	27.0	0.0	41.2	43.5	8.7	8.5	89.2	7.5
	≥1 y-o *Paralichthys olivaceus*	186.5	2.6	1.1	0.5	0.0	1.6	2.3	1.0	0.8	0.0	0.0	9.4	1.1	3.1	0.0	0.0	1.3	1.1	0.0	4.3	3.4	1.1
	Tarphops oligolepis	42.0	0.0	0.0	0.0	0.0	8.2	73.9	64.6	2.4	0.0	0.0	18.5	0.0	1.6	10.5	24.1	0.0	2.8	5.9	2.6	0.0	11.1
Soleidae	*Heteromycteris japonica*	47.7	0.0	0.0	0.0	0.0	0.0	0.8	1.4	0.0	0.0	0.0	2.4	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.0
Cynoglossidae	*Paraplagusia japonica*	136.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.4	0.9	0.0	0.0	0.0	0.0	0.0	0.0
Pleuronectidae	*Acanthopsetta nadeshnyi*	44.2	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Cleisthenes pinetorum	43.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0	17.6	0.0
	Eopsetta grigorjewi	46.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.1	0.0	0.0	0.0	0.0	0.0
	Kareius bicoloratus	104.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Limanda punctatissimus	151.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.0	0.0	0.0	0.0
	Microstomus achne	158.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.5	0.0	0.0	0.0	0.0	0.0
	Pleuronectes herzensteini	111.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0	1.0	2.7	1.8	0.0
	Pleuronectes yokohamae	62.7	1.5	2.6	0.5	21.4	18.8	15.5	3.9	4.8	8.4	15.0	7.1	70.7	68.9	37.4	23.5	15.8	21.3	10.7	2.6	32.3	6.5
Monacanthidae	*Rudarius ercodes*	25.9	0.0	0.0	0.0	0.0	3.3	78.9	14.8	0.0	0.0	0.0	3.7	0.0	0.0	11.3	7.2	0.0	0.0	2.0	0.0	0.0	4.4
	Thamnaconus modestus	80.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tetraodontidae	*Takfugu poecilonotus*	49.8	0.7	0.0	4.1	0.0	0.0	5.6	0.7	0.0	0.0	0.0	8.1	0.0	0.0	0.0	0.0	0.0	1.1	0.0	1.0	0.0	0.0
	Total		42.6	31.6	21.3	49.1	137.1	340.4	163.6	50.4	44.3	78.0	103.6	88.8	130.5	133.1	119.3	154.5	131.0	89.6	80.0	182.4	50.3

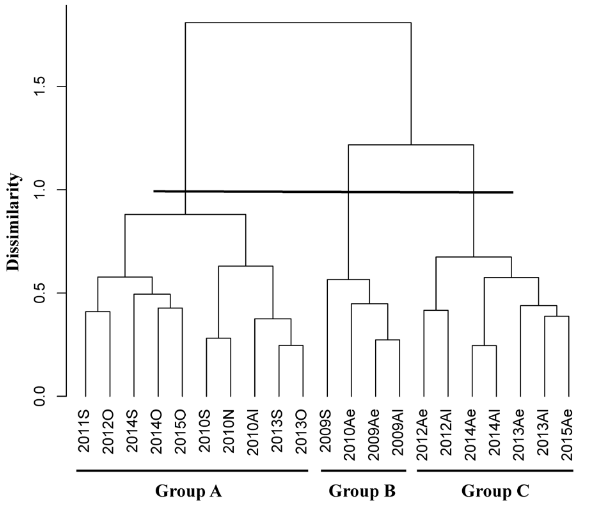

Fig. 5. Cluster dendrogram based on Bray–Curtis similarity of fish abundance data for 21 surveys from 2009 to 2015. Terminal unit indicates year and period operated: Ae, early August; Al, late August; S, September; O, October; N, November.

The overall assemblage was characterized by nine species (*Upeneus japonicus*, *Repomucenus curvicornis*, *R. lunatus*, *Pholis crassispina*, *P. nebulosa*, 0 y-o *P. olivaceus*, *Tarphops oligolepis*, *P. yokohamae* and *Rudarius ercodes*) contributing greater than 50% in cumulative SIMPER value (Table 2). The groups A, B and C contained 20, 5 and 16 key species, respectively (group A: *Okamejei kenojei*, *Conger myriaster*, *E. japonicus*, *Hypodytes rubripinnis*, *Suggrundus meerdervoortii*, *U. japonicus*, *Sillago japonica*, *R. curvicornis*, *R. lunatus*, *R. ornatipinnis*, *R. valenciennei*, *Favonigobius gymnauchen*, 0 and ≥1 y-o *P. olivaceus*, *T. oligolepis*, *Heteromycteris japonica*, *Paraplagusia japonica*, *P. yokohamae*, *R. ercodes* and *Takifugu poecilonotus*; group B: *O. kenojei*, *Occella iburia*, *Liparis agassizii*, *P. crassispina* and *P. nebulosa*; group C: *Chelidonichthys spinosus*, *Lepidotrigla microptera*, *U. japonicus*, *Pagrus major*, *O. iburia*, *Hexagrammos otakii*, *Gymnocanthus intermedius*, *Pseudoblennius cottoides*, *R. beniteguri*, *R. ornatipinnis*, *F. gymnauchen*, *P. crassispina*, 0 and ≥1 y-o *P. olivaceus*, *Cleisthenes pinetorum* and *P. yokohamae*). Ontogenetic stages of the key species were juveniles, except for *O. kenojei*, *C. myriaster*, *E. japonicus*, *L. agassizii*, *R. ornatipinnis*, *Pholis* spp. and *H. otakii*, based on total length ranges (Table 1).

Table 2. Percentage contribution from SIMPER analysis (%) and indicator value (%) for species collected during study for each survey group based on the cluster analysis.

Species	SIMPER	Indicator value (%)		
	Contribution (%)	A	B	C
Okamejei kenojei	1.7	27.4	15.8	0.0
Conger myriaster	0.4	20.0	0.0	0.0
Engraulis japonicus	3.4	39.6	0.3	0.0
Syngnathus schlegeli	0.4	5.6	11.1	0.0
Hippocampus mohnikei	1.0	14.1	0.0	8.5
Sebastes schlegeli	1.7	0.0	9.1	12.5
Hypodytes rubripinnis	1.2	20.0	0.0	0.0
Chelidonichthys spinosus	3.4	2.3	0.8	49.0
Lepidotrigla microptera	1.0	0.0	0.0	28.6
Suggrundus meerdervoortii	0.7	20.0	0.0	0.0
Upeneus japonicus	4.7	47.2	7.9	39.7
Pagrus major	1.3	4.3	0.0	33.6
Sillago japonica	0.4	20.0	0.0	0.0
Occella iburia	3.0	0.9	28.5	30.1
Hexagrammos otakii	0.7	0.0	5.4	22.4
Gymnocanthus intermedius	3.7	0.0	9.1	35.0
Pseudoblennius cottoides	2.9	6.6	5.9	47.3
Liparis agassizii	0.8	0.0	50.0	0.0
Repomucenus beniteguri	2.2	7.8	0.0	26.1
Repomucenus curvicornis	6.3	69.1	0.0	0.2
Repomucenus lunatus	5.5	78.5	0.0	0.5
Repomucenus ornatipinnis	3.1	15.5	0.0	49.3
Repomucenus valenciennei	2.6	18.1	1.9	0.3
Favonigobius gymnauchen	3.6	30.8	3.7	29.5
Pholis crassispina	4.4	10.1	34.5	28.8
Pholis nebulosa	4.5	3.4	88.6	0.0
0 y-o *Paralichthys olivaceus*	6.6	25.6	1.9	69.6
≥1 y-o *Paralichthys olivaceus*	2.9	41.5	9.0	20.5
Tarphops oligolepis	8.0	98.1	0.0	0.6
Heteromycteris japonica	1.0	40.0	0.0	0.0
Paraplagusia japonica	0.5	20.0	0.0	0.0
Cleisthenes pinetorum	1.4	0.0	0.0	28.6
Pleuronectes yokohamae	6.1	33.6	6.7	59.7
Pleuronectes herzensteini	1.1	11.6	0.0	11.9
Rudarius ercodes	5.4	80.0	0.0	0.0
Takfugu poecilonotus	2.5	28.9	11.4	0.7

3. Relationship between fish assemblage and environmental and temporal parameters

The CCA ordination based only on environmental parameters (i.e., temperature and salinity) explained 8% of variability, compared with that based on both environmental (temperature and salinity) and temporal (month and period) parameters, which explained 34% (four axes). Among four variables, only temporal parameters provided a significant explanation of the variability in the assemblage (Temp.: p=0.12; Sal.: p=0.88; month and period: p<0.01). The statistical significance of the CCA ordination model was confirmed by the Monte Carlo permutation test (p<0.001). The first two ordination axes explained 25.9% variability in fish assemblages. Eigen values of CCA for the first two axes (CCA1 and CCA2) were 0.29 and 0.17, respectively. The survey units plotted on the first two axes calculated by the CCA basically corresponded to the three groups derived from the cluster analysis. Groups A, B and C based on the cluster analysis were clearly divided into the first (mainly September to November, 2009 to 2010) and fourth quadrants (September and October, 2012 to 2015), the second quadrant

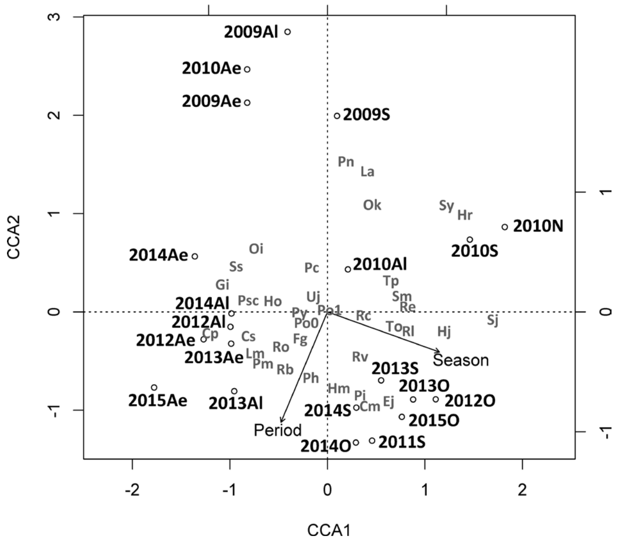

Fig. 6. CCA ordination diagram based on species abundances with temporal factors represented by vectors. Eigenvectors (Season and Period) shown by arrows indicate month and pre- or post-earthquake period, respectively. Letters with plot indicate year and period operated, corresponding to terminal unit in Fig. 5. Species abbreviations (accompanying red crosses) as follows: Cm, *Conger myriaster*; Cp, *Cleisthenes pinetorum*; Cs, *Chelidonichthys spinosus*; Ej, *Engraulis japonicus*; Fg, *Favonigobius gymnauchen*; Gi, *Gymnocanthus intermedius*; Hj, *Heteromycteris japonica*; Hm, *Hippocampus mohnikei*; Ho, *Hexagrammos otakii*; Hr, *Hypodytes rubripinnis*; La, *Liparis agassizii*; Lm, *Lepidotrigla microptera*; Oi, *Occella iburia*; Ok, *Okamejei kenojei*; Pc, *Pholis crassispina*; Ph, *Pleuronectes herzensteini*; Pj, *Paraplagusia japonica*; Pm, *Pagrus major*; Po0, 0 y-o *Paralichthys olivaceus*; Po1, ≥1 y-o *Paralichthys olivaceus*; Pn, *Pholis nebulosa*; Psc, *Pseudoblennius cottoides*; Py, *Pleuronectes yokohamae*; Rb, *Repomucenus beniteguri*; Rc, *Repomucenus curvicornis*; Re, *Rudarius ercodes*; Rl, *Repomucenus lunatus*; Ro, *Repomucenus ornatipinnis*; Rv, *Repomucenus valenciennei*; Sj, *Sillago japonica*; Sm, *Suggrundus meerdervoortii*; Ss, *Sebastes schlegeli*; Sy, *Syngnathus schlegeli*; To, *Tarphops oligolepis*; Tp, *Takigfugu poecilonotus*; Uj, *Upeneus japonicus*.

(mainly August, 2009 and 2010), and the third quadrant (mainly August, 2012 to 2015) in the relationship between axes 1 and 2, respectively (Fig. 6). The pre- and post-earthquake units were also distinct, falling on the first to second and the third to fourth quadrants, respectively. Based on the CCA ordination, both units were characterized mainly by the species complex composed of *O. kenojei*, *Syngnathus schlegeli*, *H. rubripinnis*, *L. agassizii* and *P. nebulosa*, and some callionymids and flatfish (i.e., *R. beniteguri*, *R. ornatipinnis*, *R. valenciennei*, *Paraplagusia japonica*, *C. pinetorum* and *P. herzensteini*), *C. myriaster*, *E. japonicus*, *Hippocampus mohnikei*, *C. spinosus*, *L. microptera* and *P. major*, respectively.

Discussion

In the study area, environmental factors, such as temperature and salinity, varied both seasonally and annually during summer and autumn from 2009 to 2015. Although salinity decreased temporarily in September 2011 and early August 2013, no differences were observed in salinity ranges between the pre- and post-earthquake periods. The salinity fluctuations observed in this study were essentially similar to offshore fluctuations (39°15′N, 142°00′E) recorded by Iwate Fisheries Technology Center (http://www2.pref.iwate.jp/~hp5507/kaikyou/mokuji.htm). During the summer season, an anti-clockwise circulation, flowing into the bay along the northern coast and out along the southern coast was dominant (Otobe et al. 2009). Accordingly, physical water conditions in the study area generally reflected offshore conditions. The impact of sand bar loss at the river mouth was relatively weak in terms of water condition in the study area, despite fresh water input from Unosumai River increasing temporarily due to heavy rainfall after the earthquake. Changes in the species composition related to low salinity conditions in 2011 and 2012 were indistinct, according to the CCA results.

The present results indicated that the fish assemblage in the surf zone of Otsuchi Bay is basically characterized by fish juveniles of *U. japonicus*, *R. curvicornis*, *R. lunatus*, *P. crassispina*, *P. nebulosa*, *P. olivaceus*, *T. oligolepis*, *P. yokohamae* and *R. ercodes* with seasonal changes from summer to autumn in some dominant species. While no significant differences were apparent between the pre- and post-earthquake periods in the total abundance, species richness, *H′* or physical conditions, the post-earthquake fish assemblage was apparently distinct from the pre-earthquake assemblage for both seasons, based on the cluster analysis and the CCA ordination. The data analyses indicated that the faunal structure shifted after the earthquake, depending mainly on the changes in some dominant species from *O. kenojei*, *L. agassizii*, *Syngnathus schlegeli* and *P. nebulosa* to *C. spinosus*, *L. microptera*, *P. major*, *H. otakii*, *G. intermedius*, *P. cottoides*, *R. beniteguri*, *R. ornatipinnis*, *F. gymnauchen*, 0 y-o *P. olivaceus*, *C. pinetorum*, *P. yokohamae* and *P. herzensteini*, and from *O. kenojei* and *H. rubripinnis* to *C. myriaster*, *E. japonicus*, *F. gymnauchen*, *R. ornatipinnis*, *R. valenciennei* and *P. japonica* for the summer and autumn assemblages, respectively. Shoji and Morimoto (2016) classified the fishes distributed in seagrass beds in Mangoku-ura Bay, Pacific coast of Tohoku, into (1) pelagic or migratory species, (2) sand or mud bottom-associated species and (3) seagrass or substrate-associated species based on the habitat type. According to this classification, some of the key species in the present area can be categorized as (2) and (3) for *F. gymnauchen*, *R. beniteguri*, *P. olivaceus* and *P.*

yokohamae, and *Syngnathus schlegeli*, *Pholis* spp., *H. otakii*, *P. cottoides* and *R. valenciennei*, respectively. Among the remaining key species, most of them including *C. myriaster*, *C. spinosus*, *U. japonicus*, *P. major*, *S. japonica*, *O. iburia*, *R. curvicornis*, *R. lunatus*, *R. ornatipinnis* and some flatfish, such as *T. oligolepis*, *H. japonica* and *P. japonica*, are mainly distributed in exposed surf zone habitat whereas a few, such as *H. rubripinnis*, *L. agassizii* and *R. ercodes*, occur in seagrass or macroalgal beds (Horinouchi et al. 1998, Hirai et al. 2009, Nakane et al. 2011, Yamamoto and Tominaga 2005, Mikami et al. 2012, Tomiyama et al. 2013, Wada et al. 2014). In surf zone, the fish community is not only influenced by the physical conditions, such as temperature and salinity, but also the habitat factors (Inui et al. 2010). In the study area, the community structure differed between the pre- and post-earthquake periods with a shift of species composition, due to the decrease of the seagrass or macroalgal related fishes, such as *Pholis* spp., *H. otakii*, *Syngnathus schlegeli* and *P. cottoides*, and to the increase of the epibenthic species preferring a sandy substrate, such as *F. gymnauchen* and flatfishes, the physical conditions of water temperature and salinity remaining essentially homogeneous.

Radical changes due to the 2011 tsunami in bathymetry and grain-size composition of the seafloor have been reported from various shallow waters along the ria coast of Tohoku (Goto et al. 2012). In Otsuchi Bay, the seafloor of the inner area was drastically changed, from muddy deposits to coarse-grained sand and gravels, comprising river bed sediments, due to the inundation and erosion of the sandbar near the mouth of the Unosumai River after the 2011 tsunami (Fujioka et al. 1988, Seike et al. 2013). The ecological impacts of the 2011 tsunami were proportional to the physical impacts (gauged by wave height) for less vulnerable benthic animal, resulting in varying influences on macrobenthic species (Seike et al. 2013, Urabe et al. 2013). In the innermost area of Otsuchi Bay adjacent to the study area, most of the seagrass beds were disappeared and few flowering or vegetative shoots were found after the tsunami (Komatsu et al. 2015). The results of the present study indicated that the disturbance by the tsunami also affected the fish community in Otsuchi Bay, representing an assemblage shift with the changes of the dominant species, possibly related to the drastic changes in benthic conditions.

In shallow Swedish coastal waters, mainly supporting macroalgae with ephemeral and seasonal life histories, a dramatic difference in the composition of fish species, with the replacement of dominant species, has been recorded between bare sandy and macroalgal habitats (Wennhage and Pihl 2007). The epibenthic ecosystem changed drastically, with the dominant species (flatfish and gobies) being replaced by sticklebacks, depending upon the macroalgal bloom in such habitats (influenced by a high degree of motility and the rapid redistribution following proliferation or loss of the macroalgae) (Wennhage and Pihl 2007). Flatfish juveniles prefer bare sediment for settlement, avoiding vegetated substrata which accordingly reduce their function as nursery areas (Wennhage and Pihl 1994, Wennhage 2002, Stoner and Ottmar 2003, Wennhage and Pihl 2007). Some epibenthic species, such as the gobiid genus *Pomatoschistus* and crustaceans, *Crangon crangon*, are also distributed selectively on bare sand, burying themselves under the sediment in order to avoid predators (Gibson and Robb 1992). In contrast, fish species associated with macroalgal habitats are generalized carnivores utilizing different prey types from species found in sandy beach ecosystems, which depend mainly upon benthic production (Hart and Gill 1994).

On the Swedish coast, the abundance and biomass of epibenthic fauna are greater in the areas with macroalgal mats, compared to the open sandy areas (Wennhage and Pihl 2007). McCloskey and Unsworth (2015) suggested that the disturbance of seagrass can affect the fish fauna to reduce the habitat value in the densely vegetated habitat formed in seagrass meadows. In contrast, the number of species were increased simultaneously in various flatfish juveniles (e.g., *H. japonica*, *P. japonica*, *C. pinetorum* and *P. herzensteini*) and some fishes preferring bare habitat (e.g., *P. major*, *F. gymnauchen* and *R. beniteguri*), compared with reduced numbers and variability in fishes associated with seagrass or macroalgal habitat (e.g., *Syngnathus schlegeli*, *P. nebulosa*, *H. otakii* and *P. cottoides*) after the replacement of the Otsuchi Bay surf zone substratum by sandy sediments due to the 2011 tsunami. Shallow areas of surf zones are well known to function as nursery habitats for the larval and juvenile individuals of many fish species (Robertson and Lenanton 1984, Ruple 1984, Ross et al. 1987, Santos and Nash 1995). In temperate waters, including those around Japan, vast numbers of flatfish utilize sheltered sandy beaches and sublittoral zones as nursery areas (McLachlan and Brown 2006). In the present study, juveniles of twelve flatfish species were recorded during the study period, the number of species increasing from five to ten after 2011. Among them, juveniles of three flatfish species, *P. olivaceus*, *T. oligolepis* and *P. yokohamae*, were dominant in the assemblage throughout the study period, based on the SIMPER analysis.

Significantly, the surf zone of Otsuchi Bay is also characterized by intertidal sand-burrowing peracarid crustaceans, including mysids, amphipods and isopods, which are importantly exploited by various fishes (Takahashi et al. 1999). In particular, the abundances of sand-burrowing mysids, important prey for some flatfish juveniles, such as *P. olivaceus* and *T. oligolepis*, were higher compared to other nursery grounds of *P. olivaceus* (Takahashi and Kawaguchi 1995, Yamamoto and Tominaga 2005, Tanaka et al. 2006, Tomiyama et al. 2013, Yamamoto and Tominaga 2014). The substrate replacement of due to the 2011 tsunami will likely lead to an increase of habitat, not only for the demersal fishes preferring bare sediment but also for the sand-burrowing prey organisms.

The present results indicated that the fish assemblage in the study area was characterized equally by nine dominant species, comprising juveniles of six epibenthic fishes preferring bare sediment habitat, e.g., *U. japonicus*, *R. curvicornis*, *R. lunatus*, 0 y-o *P. olivaceus*, *T. oligolepis* and *P. yokohamae*, and three species associated with seagrass or macroalgae, e.g., *Pholis* spp. and *R. ercodes*, throughout the pre- and post-earthquake periods. Thus, the fish community essentially comprises a surf zone assemblage with a few species preferring vegetated condition formed on the sandy substratum, functioning as a nursery and/or feeding ground. The expansion of bare sandy habitat due to the replacement of the substratum caused by the 2011 tsunami has appeared to magnify the fish assemblage utilizing such habitat with a reduction of the fish community associated with a vegetated habitat. Wennhage and Pihl (2007) suggested that the habitat shift from a sandy area to a vegetated state due to a macroalgal bloom reduces the ecological function and value as a nursery and feeding ground for various commercial fishes. On the contrary, the disturbance of the 2011 tsunami on the surf zone of Otsuchi Bay has affected the expansion of nursery and/or feeding potential for the flatfishes and some epibenthic fishes in the surf zone of Otsuchi Bay, including many commercial pleuronectid flatfish species, caused by the replacement of substratum by sandy sediment.

Acknowledgment

We are sincerely thank the staff of Kobayashi Set-net Fisheries Cooperative and crew of the R/V Grand Maillet for their help in collecting samples, and T. Otake, T. Kawamura and T. Kitagawa (AORI) for enabling the involvement of the research vessel in the study. We also thank G. Hardy (Ngunguru, New Zealand) and anonymous reviewers for their comments on the manuscript. This study was conducted partially with support from Grants-in-Aid for the Promotion Program for Fisheries Resources Survey in Waters around Japan from the Fisheries Agency of Japan, and Tohoku Ecosystem-Associate Marine Sciences from the Ministry of Education, Culture, Sports, Science and Technology of Japan.

Literature Cited

Able, K. W., Wuenschel, M. J., Grothues, T. M., Vasslides, J. M. and Rowe, P. M. 2013. Do surf zones in New Jersey provide "nursery" habitat for southern fishes? Environ. Biol. Fish. 96: 661–675.

Beyst, B., Hostens, K. and Mees, J. 2001. Factors influencing fish and macrocrustacean communities in the surf zone of sandy beaches in Belgium: temporal variation. J. Sea Res. 46: 281–294.

Chouinard, P. M. and Dutil, J. D. 2011. The structure of demersal fish assemblages in a cold, highly stratified environment. ICES J. Mar. Sci. 68: 1–13.

Clark, B. M., Bennett, B. A. and Lamberth, S. J. 1996. Temporal variations in surf zone fish assemblages from False Bay, South Africa. Mar. Ecol. Prog. Ser. 131: 35–47.

Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. Aust. J. Ecol. 18: 117–143.

Clarke, K. R., Somerfield, P. J. and Gorley, R. N. 2008. Testing of null hypotheses in exploratory community analyses: similarity profiles and biota-environment linkage. J. Exp. Mar. Biol. Ecol. 366: 56–69.

Colman, J. S. and Segrove, F. 1955. The tidal plankton over Stoupe Bech sands, Tobin Hood's bay (Yorkshire, North Riding). J. Anim. Ecol. 24: 445–462.

Dominguez Granda, L., Fockedey, N., De Mey, M., Beyst, B., Cornejo, M., Calderon, J. and Vincx, M. 2004. Spatial patterns of the surf zone hyperbenthic fauna of Valdivia Bay (Ecuador). Hydrobiol. 529: 205–224.

Dufrêne, M. and Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monogr. 67: 345–366.

Félix, F. C., Spach, H. L., Moro, P. S., Schwarz Jr., R., Santos, C., Hackradt, C. W. and Hostim-Silva, M. 2007. Utilization patterns of surf zone inhabiting fish from beaches in Southern Brazil. Pan-Amer. J. Aquat. Sci. 2: 27–39.

Fujioka, K., Tsukawaki, S., Yoshida, H., Yamanaka, M., Kosaka, K. and Makino, Y. 1988. Geology of Otsuchi Bay and its adjacent area—Otsuchi Bay as a natural laboratory—. Otsuchi Mar. Res. Cent. Rep. 14: 15–46 (in Japanese).

Gibson, R. N. and Robb, L. 1992. The relationship between body size, sediment grain size and the burying ability of juvenile plaice, *Pleuronectes platessa* (L.). J. Fish Biol. 40: 771–778.

Goto, K., Chague-Goff, C., Goff, J. and Jaffe, B. 2012. The future of tsunami research following the 2011 Tohoku-oki event. Sediment. Geol. 282: 1–13.

Goto, T. 2007. Comments on fisheries management and stock enhancement of Japanese flounder, *Paralichthys olivaceus*, in Iwate Prefecture based on the estimation of stock size fluctuations. Kaiyo Monthly 39: 261–267 (in Japanese).

Goto, T. 2014. Stock size fluctuations of Japanese flounder, *Paralichthys olivaceus*, in the coastal waters off Iwate Prefecture after the Tohoku earthquake and tsunami disaster. Kaiyo Monthly 46: 12–20 (in Japanese).

Goto, T. 2015. Distribution and growth of juvenile marbled sole, *Pleuronectes yokohamae*, settled in Otsuchi Bay after the Tohoku earthquake in 2011. Tohoku Demersal Fish Res. 35: 17–22 (in Japanese).

Hamerlynck, O. and Mees, J. 1991. Temporal and spatial structure in the hyperbenthic community of a shallow coastal area and its relation to environmental variables. Oceanolog. Acta, 11: 205–212.

Hammer, Ø., Harper, D. A. T. and Ryan, D. 2001. Paleontological statistics software package for education and data analysis. Palaeontl. Electr. 4: 1–9 (http://palaeo-electronica.org/2001_1/past/issue1_01.htm).

Hart, P. J. B. and Gill, A. B. 1994. Evolution of foraging behaviour in three spine stickleback. *In* The evolutionary biology of the three spine stickleback. Bell, M. A. and Foster, S. A. (eds.), pp. 207–239, Oxford University Press, Oxford

Hirai, K., Kamimura, Y., Iwamoto, Y., Morita, T. and Shoji, J. 2009. A quantitative comparison of fish assemblage between a macroalgae bed and an adjoining sandy beach in the central Seto Inland Sea. J. Grad. Sch. Biosp. Sci. 48: 1–7 (in Japanese with English abstract).

Hirose, T. and Kawaguchi, K. 1997. Spawning ecology of Japanese surf smelt, *Hypomesus pretiosus japonicus* (Osmeridae), in Otsuchi Bay, northeastern Japan. Env. Biol. Fish. 52: 213–223.

Horinouchi, M., Sano, Taniuchi, T. and Shimizu, M. 1998. Food and microhabitat resource use by *Rudarius ercodes* and *Ditrema temmincki* coexisting in a Zostera bed at Aburatsubo, central Japan. Fish. Sci. 64: 563–568.

Inui, R., Nishida, T., Onikura, N., Eguchi, K., Kawagishi, M., Nakatani, M. and Oikawa, S. 2010. Physical factors influencing immature-fish communities in the surf zones of sandy beaches in northwestern Kyushu Island, Japan. Estuar. Coast. Shelf Sci. 86: 467–476.

Iwata, M. and Numachi, K. 1981. Synecological studies in changes of animal communities in Otsuchi Bay. Otsuchi Mar. Res. Cent. Rep. 7: 35–46 (in Japanese).

Kawabata, J. 1997. Seasonal changes of fish fauna along the Pacific coast of Aomori Prefecture, Japan. Bull. Tohoku Natl. Fish. Res. Inst. 59: 83–94 (in Japanese).

Komatsu, T., Igarashi, C., Tatsukawa, K., Sultana, S., Matsuoka, Y. and Harada, S. 2003. Use of multi-beam sonar to map seagrass beds in Otsuchi Bay on the Sanriku Coast of Japan. Aquat. Liv. Resour. 16: 223–230.

Komatsu, T., Ohtaki, T., Sakamoto, S., Sawayama, S., Hamana, Y., Shibata, M., Shibata, K. and Sasa, S. 2015. Impact of the 2011 tsunami on seagrass and seaweed beds in Otsuchi Bay, Sanriku coast, Japan. *In* Marine Productivity: Perturbations and Resilience of Socio-ecosystems. Ceccaldi, H. J., Hnocque, Y., Koike, Y., Komatsu, T., Stora, G., Tusseau-Vullemin, M. H. (eds.), pp. 43–53, Springer International Publishing, Switzerland

Lock, K., Beyst, B. and Mees, J. 1999. Circadiel patterns in the tidal plankton of a sandy beach in Zeebrugge (Belgium). Belg. J. Zool. 129: 339–352.

Machado Pessanha, A. L. and Araújo, F. G. 2003. Spatial, temporal and diel variations of fish assemblages at two sandy beaches in the Sepetiba Bay, Rio de Janeiro, Brazil. Estuar. Coast. Shelf Sci. 57: 817–828.

McCloskey, R. M. and Unsworth, R. K. F. 2015. Decreasing seagrass density negatively influences associated fauna. PeerJ 3: e1053 (https://doi.org/10.7717/peerj.1053).

McLachlan, A. and Brown, A. C. 2006. The ecology of sandy shores, second ed. Academic Press, Amsterdam

Mikami, S., Nakane, Y. and Sano, M. 2012. Influence of offshore breakwaters on fish assemblage structure in the surf zone of a sandy beach in Tokyo Bay, central Japan. Fish. Sci. 78: 113–121.

Mori, N., Takahashi, T., Yasuda, T. and Yanagisawa, H. 2011. Survey of 2011 Tohoku earthquake tsunami inundation and runup, Geophys. Res. Lett. 38: 1–6.

Nakane, Y., Suda, Y. and Sano, M. 2011. Food habits of fishes on an exposed sandy beach at Fukiagehama, South-West Kyushu Island, Japan. Helgol. Mar. Res. 65: 123–131.

Okayasu, A., Shimozono, T., Yamazaki, H., Nagai, T. and Sato, S. 2013. Severe erosion of sandbar at Unosumai River mouth, Iwate, due to 2011 Tohoku tsunami. Coast. Dynam. 1013: 1311–1320.

Oksanen, J., Blanchet, G. F., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Henry, M., Stevens, H. and Wagner, H. 2013. Community ecology package. R package version 2.0–7.

Otobe, H., Onishi, H., Inada, M., Michida, Y. and Terazaki, M. 2009. Estimation of water circulation in Otsuchi Bay, Japan inferred from ADCP observation. Coast. Mar. Sci. 33: 78–86.

Pereira, H. H., Neves, L. M., da Costa, M. R. and Araújo, F. G. 2013. Fish assemblage structure on sandy beaches with different anthropogenic influences and proximity of spawning grounds. Mar. Ecol. 36: 16–27.

R Development Core Team. 2008. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria

Robertson, A. I. and Lenanton, R. C. J. 1984. Fish community structure and food chain dynamics in the surf-zone of sandy beaches: the role of detached macrophyte detritus. J. Exp. Mar. Biol. Ecol. 84: 265–283.

Ross, S. T., McMicheal Jr., R. H. and Ruple, D. L. 1987. Seasonal and diel variation in the standing crop of fishes and macroinvertebrates from a Gulf of Mexico surf zone. Estuar. Coast. Shelf Sci. 25: 391–412.

Ruple, D. L. 1984. Occurrence of larval fishes in the surf zone of a northern Gulf of Mexico barrier island. Estuar. Coast. Shelf Sci. 18: 191–208.

Santos, R. S. and Nash, R. D. 1995. Seasonal changes in a sandy beach fish assemblage at Porto Pim, Faial, Azores. Estuar. Coast. Shelf Sci. 41: 579–591.

Sasaki, R. and Nakai, K. 2006. Mark-recapture experiment using barfin flounder, *Verasper moseri* on the coast of Iwate Prefecture. Saibai Giken 34: 1–6 (in Japanese with English abstract).

Seike, K., Shirai, K. and Kogure, Y. 2013. Disturbance of shallow marine soft-bottom environments and megabenthos assemblages by a huge tsunami induced by the 2011 M9.0 Tohoku-Oki earthquake. PLoS ONE 8: e65417 (doi:10.1371/journal.pone.0065417).

Senta, T. and Kinoshita, I. 1985. Larval and juvenile fishes occurring in surf zones of Western Japan. Trans. Am. Fish. Soc. 114: 609–618.

Shannon, C. E. and Weaver, W. 1963. The Mathematical Theory of Communications. University of Illinois Press, Urbana

Shoji, J. and Morimoto, M. 2016. Changes in fish community in seagrass beds in Mangoku-ura Bay from 2009 to 2014, the period before and after the tsunami following the 2011 off the Pacific coast of Tohoku earthquake. J. Oceanogr. 72: 91–98.

Stoner, A. O. and Ottmar, M. L. 2003. Relationships between size-specific sediment preferences and burial capabilities in juveniles of two Alaska flatfishes. J. Exp. Mar. Biol. Ecol. 282: 85–101.

Takahashi, K. and Kawaguchi, K. 1995. Inter- and intraspecific zonation in three species of sand-burrowing mysids, *Archaeomysis kokuboi*, *A. grebnitzkii* and *Iiella ohshimai*, in Otsuchi Bay, northeastern Japan. Mar. Ecol. Prog. Ser. 116: 75–84.

Takahashi, K., Hirose, T. and Kawaguchi, K. 1999. The importance of intertidal sand-burrowing peracarid crustaceans as prey for fish in the surf-zone of a sandy beach in Otsuchi Bay. Fish. Sci. 65: 856–864.

Tanaka, Y., Ohkawa, T., Yamashita, Y. and Tanaka, M. 2006. Geographical differences in stomach contents and feeding intensity of juvenile Japanese flounder *Paralichthys olivaceus*. Nippon Suisan Gakkaishi 72: 50–57 (in Japanese with English abstract).

Tatsukawa, K. and Tanaka, S. 1982. Studies on the fish community in coastal waters of Otsuchi Bay. Otsuchi Mar. Res. Cent. Rep. 8: 49–68 (in Japanese).

Ter Braak, C. J. F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecol. 67: 1167–1179.

Tomiyama, T., Mizuno, T., Watanabe, M., Fujita, T. and Kawata, G. 2008. Patterns and frequency of hypermelanosis on the blind side in wild Japanese flounder. Nippon Suisan Gakkaishi 74: 171–176 (in Japanese with English abstract).

Tomiyama, T., Watanabe, M., Kawata, G. and Ebe, K. 2011. Post-release feeding and growth of hatchery-reared Japanese flounder *Paralichthys olivaceus*: relevance to stocking effectiveness. J. Fish Biol. 78: 1423–1436.

Tomiyama, T., Uehara, S. and Kurita, Y. 2013. Feeding relationships among fishes in shallow sandy areas in relation to stocking of Japanese flounder. Mar. Ecol. Prog. Ser. 479: 163–175.

Urabe, J., Suzuki, T., Nishita, T. and Makino, W. 2013. Immediate ecological impacts of the 2011Tohoku earthquake tsunami on intertidal flat communities. PLoS ONE 8: e62779 (doi: 10.1371/journal.pone.0062779).

Wada, T., Kamiyama, K., Shimamura, S., Yoshida, T., Kayaba, T. and Sasaki, M. 2013. Detection of fishing grounds, fishing season, and size distribution of stocked barfin flounder *Verasper moseri* in southern Tohoku, the Pacific coast of eastern Japan. Aquaculture Sci. 61: 39–46.

Wada, T., Osada, N., Haraguchi, H. and Uno, M. 2014. A report of fishes and marine invertebrates occurred in the surf zones of sandy beaches at eastern part of Tottori Prefecture, Honshu Japan. Bul. Tottori Pref. Mus. 51: 23–41 (in Japanese with English abstract).

Watkin, E. E. 1941. Observations on the night tidal migrant Crustacea of Kames Bay. J. Mar. Biol. Assoc. U.K. 25: 81–96.

Wennhage, H. 2002. Vulnerability of newly settled plaice (*Pleuronectes platessa* L.) to predation: effects of habitat structure and predator functional response. J. Exp. Mar. Biol. Ecol. 269: 129–145.

Wennhage, H. and Pihl, L. 1994. Substratum selection by juvenile plaice (*Pleuronectes platessa* L.): impact of benthic microalgae and filamentous macroalgae. Neth. J. Sea Res. 32: 343–351.

Wennhage, H. and Pihl, L. 2007. From flatfish to sticklebacks: assemblage structure of epibenthic fauna in relation to macroalgal blooms. Mar. Ecol. Prog. Ser. 335: 187–198.

Yamada, H., Sato, K., Nagahora, S., Kumagai, A. and Yamashita, Y. 1998. Feeding habit of the Japanese flounder *Paralichthys olivaceus* in Pacific coastal waters of Tohoku district, northeastern Japan. Nippon Suisan Gakkaishi 64: 249–258.

Yamaguchi, H., Takai, N., Ueno, M. and Hayashi, I. 2007. Changes of the trophic position of the Japanese flounder *Paralichthys olivaceus* juvenile in a sandy sublittoral area in Wakasa Bay, Sea of Japan, examined by carbon and nitrogen isotope analyses. Fish. Sci. 72: 449–451.

Yamamoto, M. and Tominaga, O. 2005. Feeding ecology of dominant demersal fish species *Favonigobius gymnauchen*, *Repomucenus* spp. and *Tarphops oligolepis* at a sandy beach where larval Japanese flounder settle in the Seto Inland Sea, Japan. Fish. Sci. 71: 1332–1340.

Yamamoto, M. and Tominaga, O. 2014. Prey availability and daily growth rate of juvenile Japanese flounder *Paralichthys olivaceus* at a sandy beach in the central Seto Inland Sea, Japan. Fish. Sci. 80: 1285–1292.

Yamashita, Y. and Aoyama, T. 1984. Ichthyoplankton in Otsuchi Bay on northeastern Honshu with reference to the time-space segregation of their habitats. Nippon Suisan Gakkaishi 50: 189–198.