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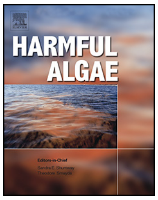

Changes in abundances of *Alexandrium tamarense* resting cysts after the tsunami caused by the Great East Japan Earthquake in Funka Bay, Hokkaido, Japan

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ABSTRACT

The 2011 Great East Japan Earthquake and the subsequent huge tsunami greatly affected both human activity and the coastal marine ecosystem along the Pacific coast of Japan. The tsunami also reached Funka Bay in northern Japan and caused serious damage to the scallop cultures there, and this tsunami was believed to have affected the coastal environments in the bay. Therefore, we investigated the changes in the spatial abundance and distribution of the toxic dinoflagellates *Alexandrium tamarense* cysts before the tsunami (August 2010) and after the tsunami (May 2011, August 2011, May 2012 and August 2012) in the bay. Further, monthly sampling was conducted after the tsunami to identify seasonal changes of *Alexandrium catenella/tamarense* cysts and vegetative cells. Significant increases were observed in the populations of *A. catenella/tamarense* cysts, comparing the abundances before the tsunami (in August 2010; 70 ± 61 cysts g^{-1} wet sediment) to those just after it (in May 2011; 108 ± 84 cysts g^{-1} wet sediment), and both *A. tamarense* bloom (a maximum density was 1.3×10^3 cells L^{-1}) and PSP (Paralytic Shellfish Poisoning) toxin contamination of scallops (9.4 mouse unit g^{-1} was recorded) occurred in the bay. Seasonal sampling also revealed that the encystment of *A. tamarense* and the supply of the cysts to bottom sediments did not occur in the bay from September to April. These results strongly suggested that the mixing of the bottom sediments by the tsunami caused the accumulation of the toxic *A. tamarense* cysts in the surface of bottom sediment through the process of redeposition in Funka Bay. Moreover, this cyst deposition may have contributed to the toxic bloom formation as a seed population in the spring of 2011.

1. Introduction

Tsunamis have affected human activity and coastal environments throughout the world. The Great East Japan Earthquake and the subsequent huge tsunami that occurred on March 11, 2011 caused catastrophic damage to human activity, buildings, and fisheries facilities in the Pacific coast of Japan, especially in the Tohoku region (Ministry of Agriculture Forestry Fisheries, 2011). This tsunami also caused many physical changes to coastal environments, and these changes have greatly influenced the coastal marine ecosystem (e.g., Akimoto et al., 2012; Tanaka, 2012; Takami et al., 2013).

The relationship between tsunamis and PSP (Paralytic Shellfish Poisoning) incidence had been empirically suspected by Japanese scientists (Fukuyo, personal communication) because the first mass PSP incident was reported with one human death at Ofunato Bay, Tohoku, Japan in 1961, just after the 1960 Chilean tsunami and earthquake (Kawabata et al., 1962). Toxic species of the genus *Alexandrium* form mandatory resting cells called ‘cysts’ and have a resting stage in the bottom sediments as part of their life cycle (Dale, 1977). Furthermore, it is known that the cysts resting on bottom sediments play an important role in initiating bloom

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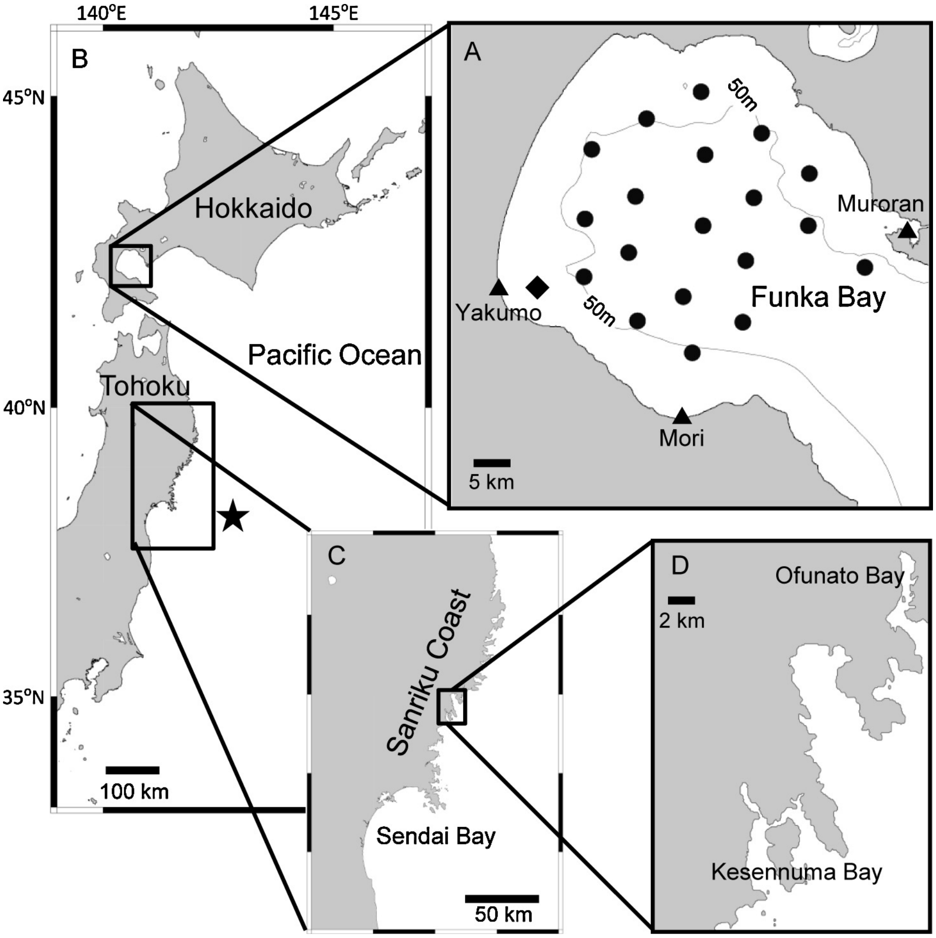

Fig. 1. Locations of sampling stations in Funka Bay (◆ indicates the Yakumo Staton, ● shows the station in the survey through the whole area of the bay, and ▲ shows the location of the cities which were introduced in the manuscript) and the Sanriku Coast where toxic *Alexandrium* blooms occurred after the 2011 tsunami.

formation in the water column (Anderson et al., 2012). Based on this background, some studies about distribution of the toxic *Alexandrium catenella/tamarense* cysts and vegetative cells were conducted along the Sanriku Coast of northeastern Japan after the 2011 tsunami. Kamiyama et al. (2014) reported the change of spatial distribution of the toxic *A. catenella/tamarense* cysts and the increase of cyst density in Sendai Bay, comparing sediment samples to those collected from the bay in 1995. Nishitani et al. (2012) also observed the bloom formation of *A. catenella* and *A. tamarense* in Kesennuma Bay and discovered an area with abundant *A. catenella/tamarense* cyst deposition in the most inner part of the bay. Similarly, Yamada et al. (2012) reported the abnormally large bloom occurrences of *A. tamarense* in Ofunato bay during the spring of 2011 and 2012 (Fig. 1, Table 1). They considered that the bottom-mixing effect of the tsunami led to the vertical and horizontal accumulation of the viable but buried *Alexandrium* cysts on the surface of bottom sediments. Thus, the accumulated cysts were able to germinate simultaneously and

Table 1
Records of the maximum densities of the toxic *Alexandrium* spp. resting cysts and vegetative cells and of the maximum toxicity of bivalves.

	Maximum density of the *A. catenella/tamarense* cysts	Maximum density of the vegetative cells of the toxic *Alexandrium* spp. from April 2011 to July 2012	Maximum toxicity of shellfish from April 2011 to July 2012 (MU = mouse unit)
Funka Bay[a]	3.2×10^2 cysts g^{-1} (May, 2011)	6.1×10^2 cells L^{-1} (*A. tamarense* in May 2011)	9.4 MU g^{-1}, scallop (*Mizuhopecten yessoensis* in June 2011)
Sendai Bay[b]	8.2×10^3 cysts cm^{-3} (June and August, 2011)	4.7×10^3 cells L^{-1} (*Alexandrium* spp. in April 2012)	50 MU g^{-1}, blue mussel (*Mytilus galloprovincialis* in April 2012)
Kesennuma Bay[c]	4.2×10^3 cysts cm^{-3} (November, 2011)	3.9×10^3 cells L^{-1} (*A. catenella* in October, 2011); 2.5×10^3 cells L^{-1} (*A. tamarense* in April 2012)	Not detected
Ofunato Bay[d]	No reference	1.0×10^5 cells L^{-1} (*A. tamarense* in May 2011); 1.4×10^4 cells L^{-1} (*A. tamarense* in April 2012)	1.4×10^2 MU g^{-1}; blue mussel (*Mytilus galloprovincialis* in June 2011; 23 MU g^{-1}; blue mussel (*Mytilus galloprovincialis* in July 2012)

Data are from:

[a] This study and the Tohoku National Fisheries Research Institute, Fisheries Research Agency (2012, 2013).

[b] Kamiyama et al. (2014) and the Tohoku National Fisheries Research Institute, Fisheries Research Agency (2012, 2013).

[c] Nishitani et al. (2012) and the Tohoku National Fisheries Research Institute, Fisheries Research Agency (2012, 2013).

[d] Yamada et al. (2012) and the Tohoku National Fisheries Research Institute, Fisheries Research Agency (2012, 2013).

initiate the large bloom observed after the tsunami. In detail, the strong bottom friction by the tsunami in shallow areas (Bernard and Robinson, 2009) was believed to cause bottom sediments to mix deeply and stir up these depositing particles, including *Alexandrium* cysts, into the water column. Then, in the redeposition process, *Alexandrium* cysts settled more slowly than other abiotic and accumulated in the surface layer. As a result, the spatial distribution and abundance of *Alexandrium* resting cysts in the surface of the bottom sediments changed after the tsunami.

Funka Bay is semi-enclosed and is located along the Pacific coast of northern Japan, with the mouth of the bay facing southeastward, an area of ca. 2.5×10^3 km^2 and a mean water depth of ca. 59 m (Fig. 1). In the bay, about 8–10 × 10^4 tons of scallop (*Mizuhopecten yessoensis*) have been harvested every year with a suspension method of aquaculture (Ministry of Agriculture Forestry Fisheries, 2007–2010), and the occurrence of the toxic *Alexandrium tamarense* and the toxin contamination of cultured scallops have mainly impacted the scallop harvesting during spring and summer (Shimada et al., 1996; Kudo et al., 2005). The huge 2011 tsunami attacked the bay (164 cm wave height in the Mori Port and 92 cm in the Muroran Port; Fig. 1; Japan Meteorological Agency, 2011) and damaged most of the facilities for scallop aquaculture (Ministry of Agriculture Forestry Fisheries, 2011). Thus, although the greatest terrestrial damage of the 2011 tsunami did not occur around the Funka Bay when compared to the Tohoku region, the coastal environments near the bay were considered to be disrupted by the tsunami.

As stated above, the 2011 tsunami was suspected to affect the distribution of the toxic *Alexandrium* cysts and the occurrence of the vegetative cells in Funka Bay. This study is aimed to evaluate the influence of the tsunami on the population dynamics of *Alexandrium* species.

2. Materials and methods

2.1. Field sampling

Sediment samples were collected at 19 stations (water depths ranging from 42 to 96 m; Fig. 1) throughout the area of Funka Bay using the T/S *Ushio-Maru* of the faculty of Fisheries, Hokkaido University in August 2010 (before the 2011 tsunami), May 2011 (just after the tsunami), August 2011, May 2012, and August 2012. Sediment samples were collected with a Smith-McIntyre grab, and three subsamples (top 0–3 cm) were taken from each grab sample using polycarbonate coring tubes (3.6-cm diameter). Subsamples were stored in plastic bottles at 2 °C in the dark before use. Water samples from layers at 0, 10, and 20 m were also obtained from the 19 stations in May 2011 and May 2012. One liter of sea-water from 0 m was collected with a plastic bucket, and those from 10 and 20 m were obtained using a rosette Niskin bottle with CTD. These samples were fixed with 0.37% formaldehyde soon after the sampling.

To identify the seasonal changes in *Alexandrium catenella/tamarense* cysts and vegetative cells, monthly sampling was conducted in one station located in the most interior part of the bay (Yakumo Station; water depth 32 m; Fig. 1) from April 2011 (after the tsunami) to December 2012. The top 0–3 cm sediment samples were obtained with a core sampler of 9-cm diameter and stored in a plastic bottle at 2 °C in the dark until use. One-liter water samples for enumeration of *Alexandrium* spp. and 500-mL water samples for measurement of nutrients were collected from 0, 10, 20, and 30 m layers using a Van Dorn water sampler. Water temperature was also monitored using a CTD (RINKO-Profiler ASTD102, JFE Advantech Co., Ltd). The samples for enumeration of *Alexandrium* spp. were fixed with 0.37% formaldehyde. The samples for nutrients analysis were filtrated with GF/F glass fiber filter (Whatman), and then the concentrations of DIN (Dissolved Inorganic Nitrogen) and DIP (Dissolved Inorganic Phosphate) were measured using a continuous flow analyzer (QuAAtro 2-HR, BL TEC K. K. and AutoAnalyzer II, Technicon Systems, Inc.).

2.2. Enumeration of the *Alexandrium* cysts and vegetative cells

The enumeration of the *Alexandrium catenella/tamarense* cysts was performed via the primuline-staining direct count method (Yamaguchi et al., 1995). Wet sediment samples (5.0 g) were suspended in distilled water and sieved through 20–150 μm plankton nets after sonication for 60 s. The size-fractionated sediment samples were suspended in 10 mL distilled water in 15-mL centrifuge tubes and fixed with 1.0% glutaraldehyde for 30 min. After centrifugation at 700 × *g* for 10 min, the pellets were suspended in 10 mL methanol in 15-mL centrifuge tubes and placed in a refrigerator for more than 24 h to remove algal fluorescent pigments. Then, methanol-suspended samples were centrifuged at 700 × *g* for 10 min, and the pellets were suspended in 9 mL distilled water and stained with 1 mL of primuline stock solution (2.0 mg mL^{-1}) for 1 h in the dark. The stained samples were centrifuged (700 × *g* for 10 min) to remove the excess primuline and supernatants, and the pellets were suspended in 10 mL distilled water. After repeating this washing by centrifugation, the pellets were finally diluted to 10.0 mL total with distilled water for microscopic observations. Samples (0.2 mL) were placed uniformly on slides and observed with an inverted epifluorescence microscope (Eclipse TE200, Nikon Co.) under excitation by blue light (450–490 nm). Three subsamples were counted for each sample, and the cyst densities (per g wet sediment) were calculated from the average value of the counts. The specific gravity of sediments collected at Yakumo station in every sampling occasion was determined simply from the volume and weight of sediment (Kamiyama, 1996). Using the value of the specific gravity, the unit of cyst densities at the Yakumo station was converted from per g wet sediment to per cm^{-3} wet sediment.

Fixed sea-water samples were concentrated 100× by the settling method (Utermöhl, 1958). *Alexandrium* vegetative cells were stained with fluorescent dye (Calcofluor white M2R; Fritz and Triemer, 1985). Stained subsamples (1 mL) were observed with an inverted epifluorescence microscope (Eclipse TE200, Nikon) under UV light excitation (365 nm) for species identification due to morphological character of the thecal plate and enumeration of vegetative cells of the genus *Alexandrium*. It is impossible to distinguish between cysts of *Alexandrium tamarense* and *Alexandrium catenella* by morphological observation using a microscope (Fukuyo, 1985). However, vegetative cells were only detected as *A. tamarense* type in this study (having a ventral pore), and Miyazono et al. (2012) reported that all cysts collected from a sediment core sample in Funka Bay before the 2011 tsunami were genetically identified as *A. tamarense*. Therefore, we regarded the cysts and vegetative cells present in the bay as *A. tamarense*.

2.3. Statistical analysis

Statistical analyses were conducted to detect changes in the abundance and distribution of the samplings through Funka Bay. Seasonal differences in the cyst abundances at each station were analyzed by a multiple comparison by Wilcoxon's signed-rank test with Bonferroni correction. Wilcoxon's signed-rank test was also performed to compare the abundances of the vegetative cells throughout Funka Bay between May 2011 and May 2012. To identify the tendency of the geographic distribution of the cysts and vegetative cells throughout the bay, Mantel test (Sokal and Rohlf, 1995) of association between a difference of cysts or

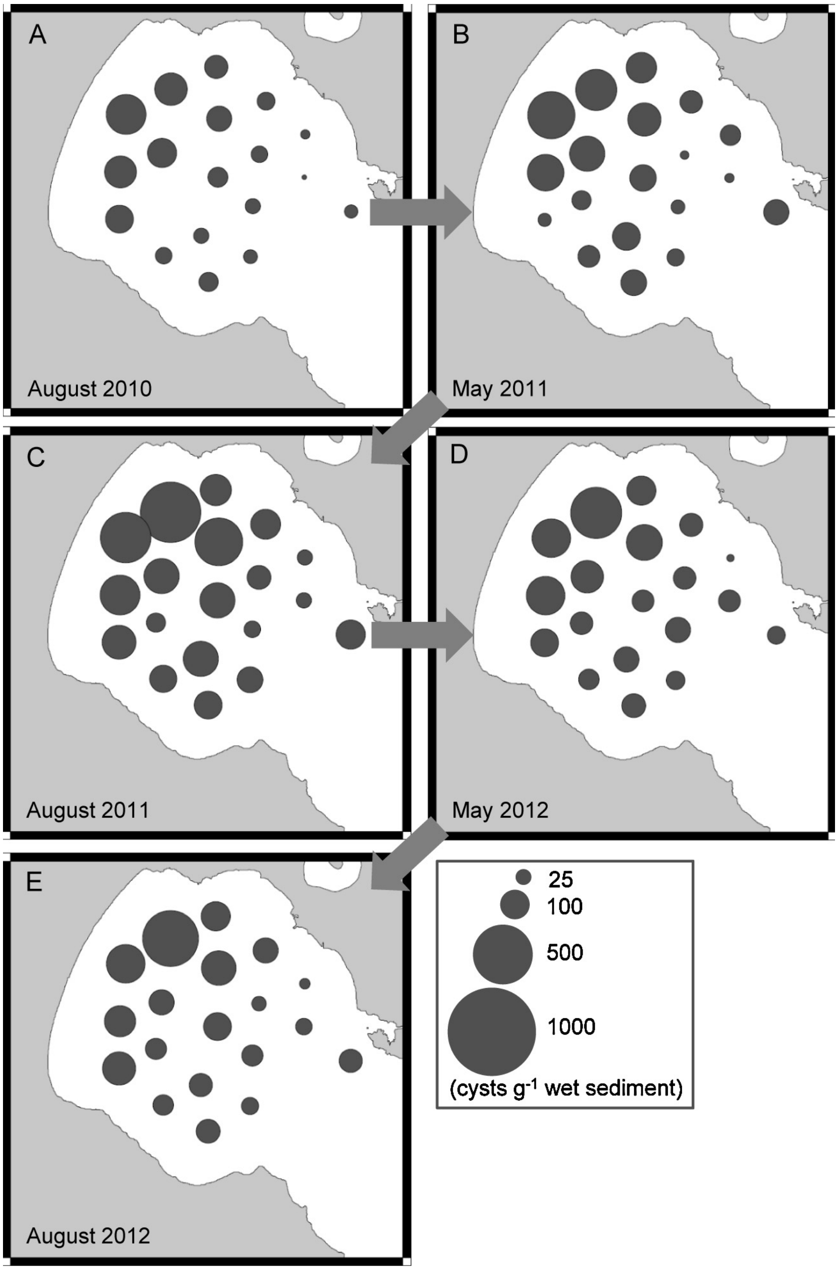

Fig. 2. Seasonal changes in the abundances and spatial distribution of the *A. catenella/tamarense* resting cysts (cysts g^{-1} wet weight) throughout Funka Bay in August 2011 (A), May 2011 (B), August 2011 (C), May 2012 (D), and August 2012 (E).

vegetative cells density and a geographic distance matrix was carried out in each sampling period.

3. Results

3.1. *Comparison of spatial abundances and distributions of the* Alexandrium tamarense *cysts and vegetative cells*

Fig. 2 shows the changes in the spatial abundance and distribution of the resting cysts of *Alexandrium tamarense* in Funka Bay from August 2010 to August 2012, and Table 2 shows comparisons between sampling periods of the cyst abundances with Wilcoxon's signed-rank test and of the cyst distribution by the Mantel test. The cyst abundances significantly increased between August 2010, just before the tsunami, and May 2011, just after the tsunami ($p < 0.05$), and from May 2011 to August 2011 ($p < 0.05$). Then, a significant decrease in the cyst abundance was observed from August 2011 to May 2012 ($p < 0.05$). In all sampling periods after the tsunami, cysts abundances were significantly higher than that of before the tsunami.

The Mantel test showed significant correlation between the geographic distance and the difference of the cyst densities in the sampling periods of August 2010, May 2011, August 2011, and May 2012 (Table 1B). Fig. 2 shows that *Alexandrium* cysts tended to exist at high density in the inner (northwest) part of the bay during these periods.

Spatial abundance and distribution of *Alexandrium tamarense* vegetative cells in each water depth (0, 10, and 20 m) are presented in Fig. 3. The Wilcoxon's signed-rank test showed a significant difference between the abundances of the vegetative cells in May 2011 and May 2012 ($p < 0.0001$). *A. tamarense* occurred widely throughout the bay in May 2011 (average cell density ± SD, $1.9 \times 10^2 \pm 2.1 \times 10^2$ cells L^{-1}), whereas the occurrence of *A. tamarense* vegetative cells in May 2012 (average cell density ± SD,

Table 2
Results of multiple comparison by Wilcoxon's signed-rank test with Bonferroni correction (A) and Mantel test (B).

Sampling period	Mean cyst density ± SD (cysts g^{-1} wet weight)	p value			
		May 2011	August 2011	May 2012	August 2012
(A) Wilcoxon's signed-rank test with Holm correction					
August 2010	70 ± 61	$p < 0.05$	$p < 0.01$	$p < 0.01$	$p < 0.01$
May 2011	108 ± 84		$p < 0.05$	$p > 0.1$	$p > 0.1$
August 2011	165 ± 127			$p < 0.05$	$p < 0.01$
May 2012	117 ± 87				$p > 0.1$
August 2012	112 ± 98				
(B) Mantel test					
Cysts	August 2010	$p < 0.01$			
	May 2011	$p < 0.01$			
	August 2011	$p = 0.04$			
	May 2012	$p = 0.02$			
	August 2012	$p = 0.14$			
Vegetative cells	May 2011	$p = 0.35$			
	May 2012	$p = 0.90$			

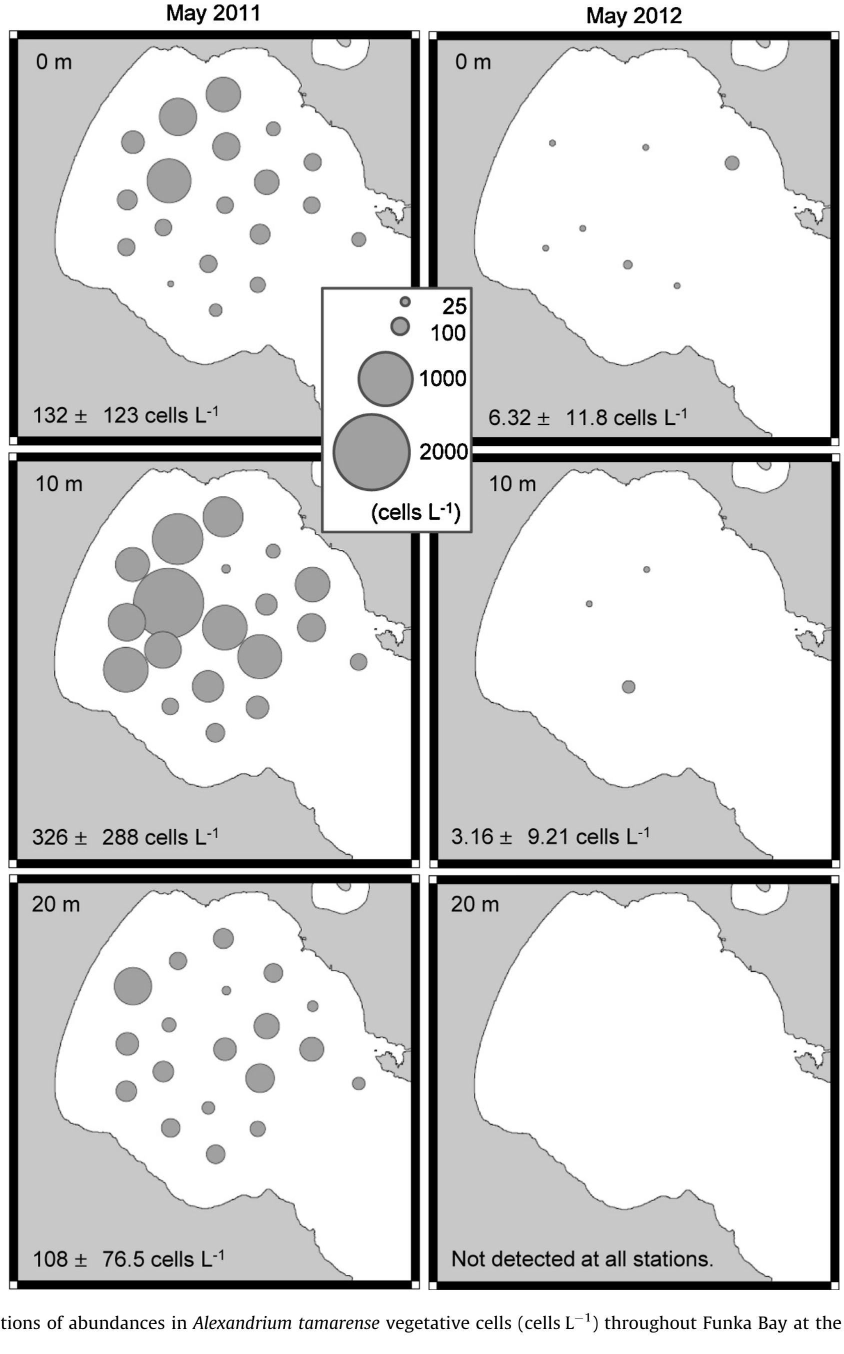

Fig. 3. Spatial distributions of abundances in *Alexandrium tamarense* vegetative cells (cells L^{-1}) throughout Funka Bay at the 0, 10 and 20 m layers.

6.3 ± 9.1 cells L^{-1}) was substantially lower than that in May 2011. The Mantel test did not show the significant correlation between geographic distance and difference of the vegetative cell densities in these two years.

3.2. Seasonal changes of Alexandrium tamarense *vegetative cells, cysts at the Yakumo station*

Alexandrium tamarense vegetative cells were first detected in April 2011 (20 cells L^{-1} in the surface layer) and were most dense in June (maximum cell density, 3.4×10^2 cells L^{-1} in 0 m; Fig. 4). Vegetative cells were only detected in the 30-m layer from July to August (10 cells L^{-1} and 20 cells L^{-1}, respectively) and were not detected from September 2011 to February 2012. They were present from March to July in 2012, and their abundances were lower than those from 2011 (maximum cell density in 2012 was 40 cells L^{-1} in July at 20 m).

The highest density of *Alexandrium tamarense* resting cysts (1.3×10^2 cysts cm^{-3} wet sediment) was detected at the first sampling time (April 2011, just after the 2011 tsunami). Then, cyst density drastically decreased until June 2011 (2.1×10^1 cyst cm^{-3} wet sediment), whereas the density of the vegetative cells increased. The density of the *A. tamarense* resting cysts sharply recovered from June to July (1.2×10^2 cysts cm^{-3} wet sediment) and gradually decreased during the time from August 2011 to June 2012. After a slight increase in cyst density from July to September 2012, it gradually decreased until December.

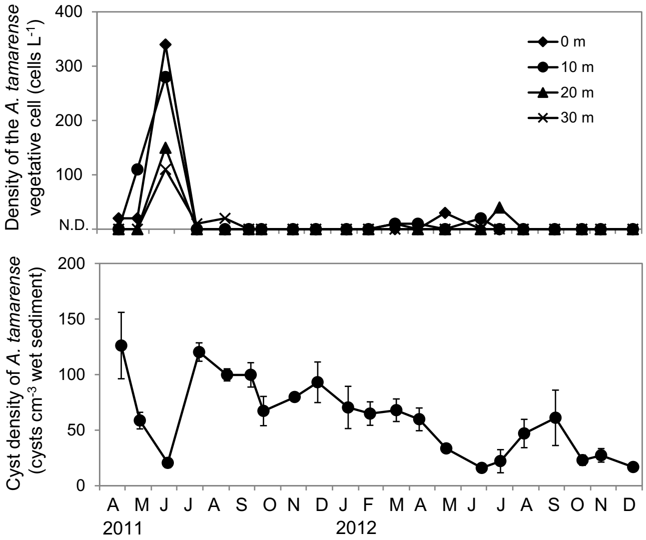

Fig. 4. Seasonal changes in *Alexandrium tamarense* vegetative cells (cells L^{-1}) and resting cysts (cysts cm^{-3} wet weight) at the Yakumo station from April 2011 to December 2012. Error bars show standard deviation.

Seasonal changes in water temperature, DIN, and DIP are shown in Fig. 5. Water temperature ranged from 2.3 to 22.9 °C. DIN and DIP concentrations ranged from <0.01 μM to 10.7 μM and from 0.02 μM to 0.95 μM, respectively, and DIN concentration reached at lowest level from spring to summer including the period during *Alexandrium tamarense* appeared. Significant annual fluctuation of the water temperature and the nutrients between 2011 and 2012 were not observed.

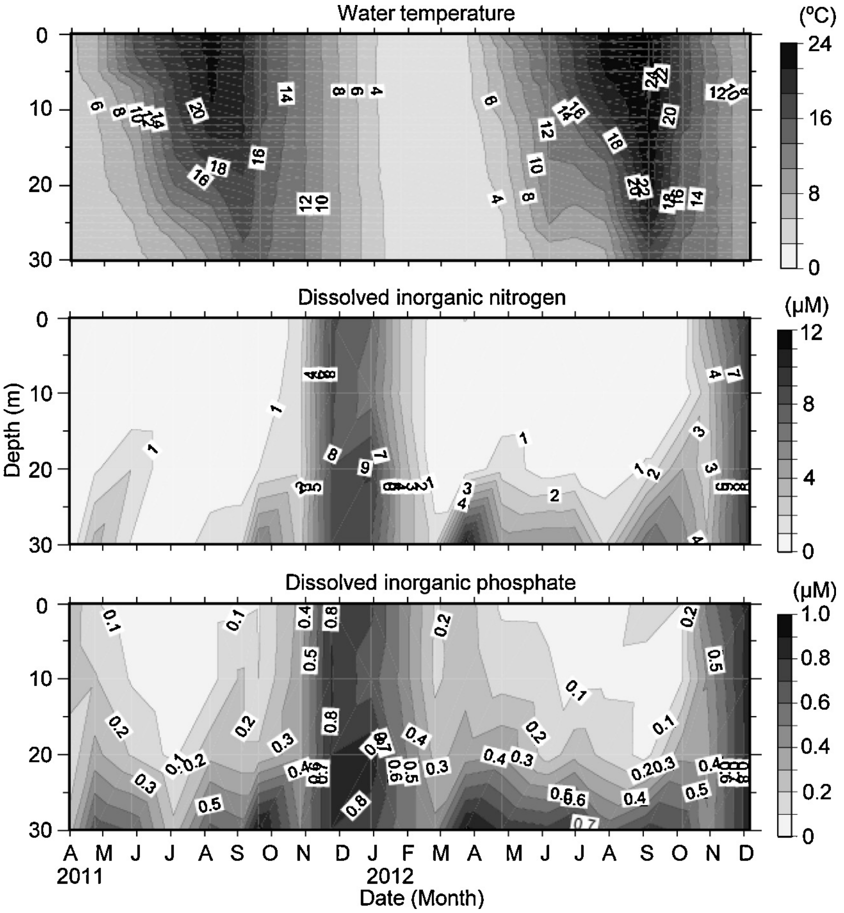

Fig. 5. Seasonal changes of water temperature, dissolved inorganic nitrogen and dissolved inorganic phosphate at the Yakumo station from April 2011 to December 2012.

4. Discussion

4.1. Increase of the Alexandrium tamarense resting cyst before and after the 2011 tsunami in Funka Bay

Typically, it is assumed that the main causes of increasing abundances of cysts in the bottom sediments are increase in the supply of cysts by encystment of the vegetative cells from a water column and accumulation by hydrological transport in the deposition process (Anderson et al., 2012). In Funka bay, it was known that *Alexandrium tamarense* only bloomed during spring to early summer (Uchida et al., 1980; Nishihama, 1985; Shimada et al., 1996). The present study also found no *A. tamarense* vegetative cells in the water column from September to February. Therefore, supplying abundant cysts from the water column into the bottom sediments by the encystment of vegetative cells did not occur in Funka Bay from autumn to winter. In the present study, relative high densities of *A. tamarense* cysts were only observed from July 2011 to September 2011 and in September 2012 in the seasonal sampling (Fig. 4) and from the August 2011 sampling throughout the bay (Table 2A and Fig. 2C). Thus, increases in the cyst abundances were only found after the occurrences of the vegetative cells except after the tsunami (Figs. 3 and 4). Moreover, a decrease in the cyst abundance from autumn to spring was observed in both the seasonal sampling (Fig. 4) and the wide area survey in August 2011 and May 2012 (Table 2A, Fig. 2C and D). This suggests that it is impossible to supply the large amounts of newly formed cysts from water columns in Funka Bay from autumn to the next spring under normal circumstances.

It is well known that *Alexandrium* cysts are strongly affected by hydrological transportation during the deposition process, and this mechanism causes local accumulation of the cysts (for example, White and Lewis, 1982; Turgeon et al., 1990). Therefore, hydrological transportation in Funka Bay may increase the local *Alexandrium tamarense* cyst density. This study showed that the densest cyst deposition likely occurred in the innermost part of the Bay (Table 2 and Fig. 2), but the heterogeneous cyst distribution in the bay was observed both before and after the tsunami, and an increase of cyst densities after the tsunami was found at most stations throughout the bay (17 of 19 sampling stations). Therefore, the increase of the cyst abundance after the 2011 tsunami occurred regardless of the accumulation by hydrological transportation.

Results presented here suggest that the increase of cyst abundance throughout the bay just after the 2011 tsunami cannot be explained by the supply of cysts from the encystment of the vegetative cells and the accumulation by the hydrological transportation. Further, it strongly suggested that this 'abnormal' increase in the cysts in the bay was due to the bottom-mixing effect by the 2011 tsunami, which affected the vertical distribution of the depositing *Alexandrium tamarense* cysts. Miyazono et al. (2012) investigated the vertical distribution and survivability of the *A. tamarense* resting cysts in a sediment core in Funka Bay before the 2011 tsunami. They discovered abundant viable cyst deposition in the deeper layer and over 100-year survival of some of the cysts that were collected from the approximately 30-cm depth of the sediment core. Moreover, Shimada and Miyazono (2005) collected the top 0–3 cm sediment samples from 60 stations throughout Funka Bay in July 1999 and reported abundant *A. tamarense* cyst deposition (mean cyst density ± SD, 503 ± 392 cysts g^{-1} wet sediment). These studies proved that abundant cysts of *A. tamarense* were distributed in the deeper layer of the bottom sediments before the tsunami. This abundant cyst deposition was considered to be stirred up into resuspension by the tsunami and to accumulate in the surface layer during redeposition.

The maximum density of the *Alexandrium* cyst after the tsunami in Funka Bay was about one order of magnitude smaller than that in the Sendai Bay and the Kesennuma Bay (Table 1). The wave height in the Funka Bay (164 cm in Mori Port and 92 cm in Muroran Port) was much lower than observations from the Pacific coast of the Tohoku region such as the Sendai Bay and the Ofunato Bay (over 8.6 m and 8.0 m, respectively; Japan Meteorological Agency, 2011). This comparison suggests that the magnitude of a tsunami highly affects the succeeding depth of bottom mixing and the magnitude of the accumulation of the cysts.

4.2. Effect of the 2011 tsunami on the spatial distribution of Alexandrium tamarense resting cysts

The present study revealed that *Alexandrium tamarense* resting cysts increased in abundance in 17 of 19 sampling stations in Funka Bay after the 2011 tsunami (Fig. 2A and B), strongly suggesting that redeposition of cysts by the tsunami occurred widely throughout the bay. When a tsunami arising in a deep ocean reaches shallow areas, where the water depth is less than 50 m, the effect of bottom friction becomes very strong (Bernard and Robinson, 2009). The bottom-mixing effect of the tsunami affected the whole area studied because Funka Bay is surrounded by shallow areas, where the water depth is less than 50 m, except for the mouth of the bay, to the south-east (Fig. 1).

Wave height of a tsunami is affected by several geophysical features. For example, tsunamis are amplified in the inner part of a rectangular, V form, or shoal bay (Bernard and Robinson, 2009). Kamiyama et al. (2014) reported that abundant cyst distribution moved to the west side (inner part of the bay) in the Sendai Bay, which is a rectangular bay, unlike the spatial distribution of *Alexandrium* cysts in the Sendai Bay in 2005. In addition, Nishitani et al. (2012) discovered an abundant cyst deposition 'hot spot' in the innermost part of Kesennuma Bay, which is a prototypical V form bay, after the 2011 tsunami. These reports indicate that the accumulation of cysts by a tsunami tends to be more pronounced in the inner part of the bay than the outer part. In the present study, more cysts were distributed in the innermost part of Funka Bay after the tsunami (May 2011). However, this tendency had already existed before the tsunami (August 2010, Fig. 2 and Table 2), and there is no evidence that the tsunami affected the spatial distribution of the *Alexandrium* cysts in Funka Bay.

4.3. Influence on the incidence of vegetative cells and on cyst formation after the tsunami

In Sendai Bay, Kesennuma Bay, and Ofunato Bay, where the 2011 tsunami caused catastrophic damage, subsequent dense blooms of *Alexandrium tamarense* reached the highest densities ever recorded in those areas (Table 1). These facts suggest that bottom-mixing effects by the 2011 tsunami supplied many viable cysts to surficial bottom sediments that functioned as seed populations for the blooms. Similarly, a relatively large bloom of *A. tamarense* was observed throughout Funka Bay (Figs. 3 and 4), and there was a subsequent eight-month warning to scallop aquaculture of the PSP toxin contamination in 2011 after the tsunami (Tohoku National Fisheries Research Institute, Fisheries Research Agency, 2012). However, the bloom magnitude and cyst density in Funka Bay after the tsunami were much lower than those in Sendai Bay, Kesennuma Bay or Ofunato Bay, which belong to the Sanriku Coast (Table 1). The Sanriku Coast was close to the epicenter of the 2011 Tohoku Earthquake, and larger tsunami waves (wave height was more than 10 m) hit in these areas than in Funka Bay. Therefore, the influence of accumulating *Alexandrium* cysts on the bottom surface was considered dependent on the scale of the tsunami.

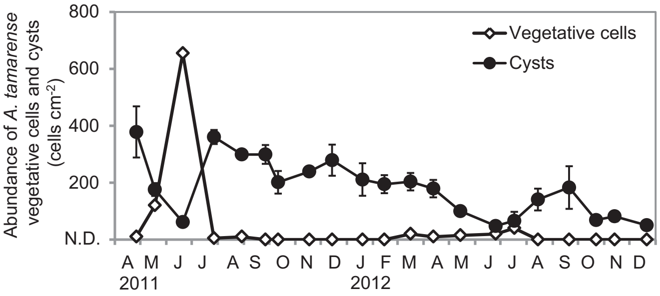

Fig. 6. Seasonal changes in the cell abundances of *Alexandrium tamarense* vegetative cells and resting cysts (cells cm^{-2}) at the Yakumo station from April 2011 to December 2012. Data of the abundances show accumulated data in water column (0–30 m) and sediment column (0–3 cm), respectively.

The incidences of the vegetative cells drastically reduced in 2012, compared with the bloom in 2011. Moreover, the cyst abundance was slightly decreased in the bay after August 2011. Decreasing populations of *Alexandrium tamarense* vegetative cells and cysts suggest that the effect of the tsunami on the *Alexandrium* population was limited to 2011, at least for Funka Bay.

In resuspending bottom sediments by the tsunami, large amounts of "stored" nutrients might be released in the water column and contribute to growth of *Alexandrium tamarense*. However, significant increases or changes in water quality including DIN and DIP were not observed after the tsunami (Fig. 5). Therefore, the contributions of the released nutrients to occurrence of the *A. tamarense* bloom were considered to be low or not to exist in Funka Bay.

After the *Alexandrium tamarense* bloom in Funka Bay during May 2011 and June 2011, an increase in depositing cyst abundance was observed temporarily throughout the bay in August 2011. Fig. 6 shows seasonal distribution of the *A. tamarense* vegetative cells and cysts abundances per unit area (cm^{-2}) at the Yakumo station. The abundances show accumulated data in water column (0–30 m) and sediment column (0–3 cm), respectively. After vegetative cells was at a peak with 6.6×10^2 cells cm^{-2} in June 2011, sudden increase of the cysts reached 3.0×10^2 cysts cm^{-2} in July 2011. Previous studies reported that cyst formation rate of *A. tamarense* was about 20–40% (Anderson et al., 1984; Anderson and Lindquist, 1985; Ichimi et al., 2001). In this study, cyst formation rate calculated from data in June 2011 and July 2011 (45%) is not largely different from the values in previous reports. Furthermore, the optimum temperatures of encystment of *A. tamarense* were reported as 21 and 14 °C (Anderson et al., 1984; Nagai et al., 2004). Water temperature at surface layer rose over 14 °C in June 2011 at Yakumo station (Fig. 5). Therefore, it is strongly suggested that sudden increase of the cyst abundance in July 2011 was due to cyst formation of the vegetative cells in water column.

Cyst densities at Yakumo station gradually decreased during July 2011 and March 2012 and reached 54% of its peak (Figs. 4 and 6). It is suggested that supply of the cysts by encystment or loss of the cysts by germination did not occur in this period, because *Alexandrium tamarense* vegetative cells were not detected in the water column during this period. Although it is still unclear why the cyst densities decreased from summer to winter, this reason may be explained as natural decrease, such as natural death, consumption by deposit feeders, transport by turbulence, or sedimentation.

5. Conclusion

The present study revealed an aberrant increase in the abundance of *Alexandrium tamarense* resting cysts on the surface of bottom sediments in Funka Bay after the 2011 huge tsunami caused by the Great East Japan earthquake, most likely caused the accumulation of *A. tamarense* cysts on the bottom surface during the process of redeposition. Moreover, this increased accumulation of viable cysts contributed to the toxic blooms that contaminated cultured scallops in 2011. The tsunami was believed to cause the occurrences of the toxic *A. tamarense* blooms in large areas affected by the wave, including most of the Pacific coast of northern Japan.

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