



Prevalence and species richness of trematode parasites only partially recovers after the 2011 Tohoku, Japan, earthquake tsunami

Osamu Miura^{a,*}, Gen Kanaya^b, Shizuko Nakai^c, Hajime Itoh^{b,d}, Satoshi Chiba^e

^a Faculty of Agriculture and Marine Science, Kochi University, 200 Monobe, Nankoku, Kochi 783-8502, Japan

^b National Institute for Environmental Studies, 16-2 Onogawa, Tsukuba, Ibaraki 305-8506, Japan

^c Department of Marine Science and Resources, College of Bioresource Sciences, Nihon University, 1866 Kameino, Fujisawa, Kanagawa 252-0880, Japan

^d Atmosphere and Ocean Research Institute, The University of Tokyo, 5-1-5 Kashiwanoha, Kashiwa, Chiba 277-8564, Japan

^e Division of Ecology and Evolutionary Biology, Graduate School of Life Sciences, Tohoku University, Sendai, Miyagi 980-8578, Japan

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ABSTRACT

Trematode parasites have complex life cycles and use a variety of host species across different trophic levels. Thus, they can be used as indicators of disturbance and recovery of coastal ecosystems. Estuaries on the Pacific coast of northeastern Japan were heavily affected by the 2011 Tohoku earthquake tsunami. To evaluate the effect of the tsunami on the trematode community, we examined trematodes in the mud snail, *Batillaria attramentaria*, at five study sites (three sites severely exposed to the tsunami and two sites sheltered from the tsunami) in Sendai Bay for 2 years prior to and 8 years after the tsunami. While the trematode prevalence decreased at all study sites, the species richness decreased only at the sites exposed to the tsunami. Although parasitism increased over the study period post-tsunami, the community had not fully recovered 8 years after the event. Trematode community structure has changed every year since the tsunami and has not stabilised. This could be explained by the alteration of first and second intermediate host communities. Our study suggests that it will take more time for the recovery of the trematode community and the associated coastal ecosystem in the Tohoku region.

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1. Introduction

By inundating coastal habitats with massive amounts of water, tsunamis can cause large disturbances to coastal organisms (Ramachandran et al., 2005; Sri-Aroon et al., 2006; Lomovasky et al., 2011; Jaramillo et al., 2012). Tsunamis inundate coastal organisms and alter habitat structure and abiotic conditions (Lomovasky et al., 2011; Jaramillo et al., 2012; Seike et al., 2016).

On 11 March 2011, an earthquake off the coast of the Tohoku, Japan, generated tsunami waves that struck the Pacific coast of northeastern Japan. Tsunamis more than 10 meters high were recorded at many bays, beaches and rocky shores along the coasts in Iwate, Miyagi and Fukushima Prefectures (Mori et al., 2011). These tsunamis devastated coastal areas and affected coastal organisms (see review in Miura and Kanaya, 2017). For example, Kanaya et al. (2012) reported that approximately 40% of macrobenthic species were eliminated from Gamou Lagoon after the tsunami. Similarly, Urabe et al. (2013) showed that 30–80% of the macrobenthos at the tidal flats in Sendai Bay area disappeared after

the tsunami. Even though half of the species recorded before the tsunami were also present after the tsunami, their population sizes were greatly reduced (see Kanaya et al., 2012; Miura et al., 2012).

The tsunami can have long-term effects on coastal ecosystems. Since trematode parasites have complex life cycles and infect multiple hosts in different trophic levels (Galaktionov and Dobrovolskij, 2003), they can be used as indicators of disturbance and recovery of coastal ecosystems (Huspeni and Lafferty, 2004; Huspeni et al., 2005). The diversity and abundance of trematodes in first intermediate hosts are generally positively correlated with the diversity and abundance of final host birds (Hechinger and Lafferty, 2005) and with those of macrobenthos that potentially serve as second intermediate hosts for trematodes (Hechinger et al., 2007). Therefore, disturbances negatively affecting intermediate or definitive hosts should cause a decline in trematodes in first intermediate host snails. Several studies directly assessed the association of disturbances with trematode parasitism in snail populations. Keas and Blankespoor (1997) found considerable reductions of trematodes in lake snails after environmental degradation caused by human activities. Similarly, Huspeni and Lafferty (2004) found that snails in a degraded environment had significantly fewer trematodes than those in intact control sites,

* Corresponding author.

E-mail address: miurao@kochi-u.ac.jp (O. Miura).

but the trematode communities gradually became similar after restoration. Natural disturbances such as hurricanes also affect the trematode community. Aguirre-Macedo et al. (2011) reported that trematode diversity and abundance in mud snails significantly decreased after a hurricane and it took several years for the trematode populations to recover. In our study, we predicted that the trematode community in snails would be affected by the tsunami through the loss and decreased availability of hosts, and would not recover without the recovery of host populations.

Batillaria attramentaria was one of the most abundant macro-organisms on the mud flats in the Tohoku region but densities were reduced after the tsunami (Miura et al., 2012, 2017). *Batillaria attramentaria* serves as the first intermediate host of eight trematode species that use a variety of second intermediate and definitive host species (Hechinger, 2007). Thus, this snail-trematode system provides an opportunity to examine negative effects of the tsunami on the estuarine ecosystem. Here, we compare trematode prevalence and species richness in *B. attramentaria* before and after the tsunami to determine how the tsunami affected the trematode community. We examined this snail-trematode system for 2 years before the tsunami and 8 years after the tsunami to monitor the decline and recovery of the trematode community and the associated coastal ecosystem.

2. Materials and methods

We collected *B. attramentaria* from five tidal flats in Sendai Bay (Fig. 1) in 2005 and 2006 before the tsunami and 2012–2019 after the tsunami. Sampling was mainly conducted between April and June, but it was done in February in 2006. We used the quadrat method described in Miura et al. (2012) to collect snails haphazardly. Due to the strong reduction in snail densities due to the tsunami (Miura et al., 2012), it was often necessary to search a wider area surrounding each sampling site to acquire a sufficient number of snails after 2012. The snails were transported back to the laboratory and dissected under a stereo-microscope. We identified trematode species based on Hechinger (2007). We did not differentiate *Philophthalmid* sp. I and sp. II, and dealt with them as *Philophthalmid* spp. since they are not easily differentiated when they are immature. All these trematodes utilise various intertidal and subtidal organisms as their second intermediate hosts and infect mainly shore birds as definitive hosts (Table 1).

A tsunami is expected to severely affect the trematode community. However, the trematode community can change over time due to a variety of factors (Esch et al., 1997, 2001). Unfortunately, we do not have control sites which have not experienced the 2011 tsunami. However, it is still possible to evaluate the effect of the tsunami by comparing the sites exposed to the tsunami with the sites sheltered from the tsunami. In our sampling sites, Nagatsuraura, Katsugigaura and Torinoumi were substantially affected by the tsunami, with the destruction of many houses and infrastructure. On the other hand, the sampling sites at Mangokuura and Matsukawaura were located at the inner parts of the bays and were not strongly affected by the tsunami. Therefore, we compared the trematode prevalence and species richness at the exposed and sheltered sites, with the aim of evaluating the effect of the tsunami on the trematode communities.

Snails larger than 15 mm in length were used for the analyses of parasitism to reduce the effects of host size on infection by trematode species. We used the jackknife estimator to estimate the trematode species richness (Walther and Morand, 1998; Zelter and Esch, 1999) using EstimateS v.9.1.0 (<http://purl.oclc.org/estimates>). To make the most useful comparisons, we consistently resampled 49 individuals within each population. The samples from Torinoumi and Mangokuura in 2013, and those from Mat-

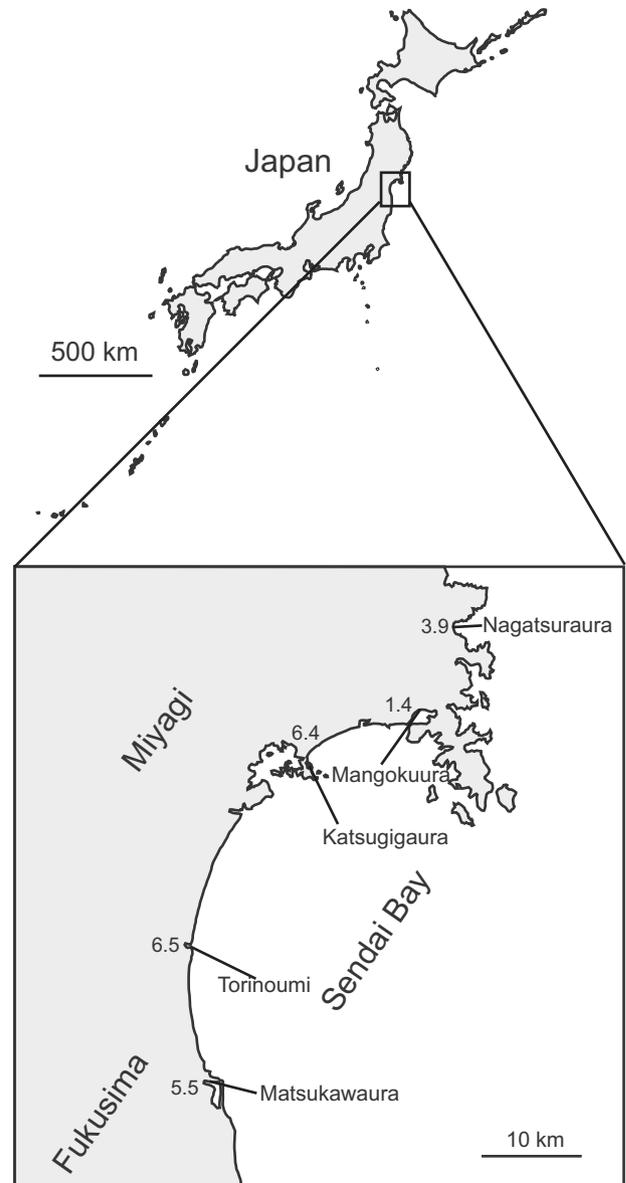


Fig. 1. The map of sampling sites in Sendai Bay, Tohoku region, Japan (Nagatsuraura site: 38°33'26.7"N, 141°27'27.7"E; Mangokuura site: 38°25'39.6"N, 141°22'44.3"E; Katsugigaura site: 38°20'52.9"N, 141°09'16.0"E; Torinoumi site: 38°01'51.1"N, 140°54'31.4"E; Matsukawaura site: 37°49'22.9"N, 140°57'23.2"E). Numbers next to sampling sites indicate inundation heights of the tsunami (m) (recorded at closest location to each site), based on Mori et al. (2011).

sukawaura in 2016, were excluded from the analysis due to their small sample sizes.

We used a Cochran-Mantel-Haenszel test to compare the trematode prevalence among years, controlling for the effect of sites. We also used a general linear mixed model to compare the trematode species richness before and after the tsunami. Site and sampling year were treated as random effects. The analyses were performed using JMP v.9.0 (SAS, Institute).

To track the changes in each trematode community, we built a similarity matrix based on the Bray-Curtis distance using the trematode species prevalence for each population. The dataset was square-root transformed to avoid overcontributions of dominant species. Populations with less than 5% overall prevalence were excluded from this analysis. The similarity matrix was visualised on a two-dimensional graph using non-metric multidimensional scaling (nMDS).

Table 1

Trematode species which appeared in this study. Their overall prevalences are also shown. Their potential second and definitive host information was based on Gibson et al. (2002), Jones et al. (2005), Hechinger (2007), Bray et al. (2008).

Family	Species	Overall prevalence	Inferred second intermediate host	Inferred definitive host
Himasthliidae	<i>Acanthoparyphium</i> sp. 1	1.6	Mollusks, polychaetes	Birds
Heterophyidae	<i>Cercaria batillariae</i>	29.2	Fishes	Birds, fishes, mammals
Microphallidae	<i>Cercaria hosoumininae</i>	2.8	Crustaceans	Birds
Cyathocotylidae	<i>Cyathocotylid</i> sp. 1	0.2	Fishes	Birds, reptiles, mammals
Philophthalmidae	<i>Philophthalmid</i> spp.	1.9	Mollusks	Birds, occasionally mammals and reptiles
Renicolidae	<i>Renicola</i> sp. 1	0.7	Mollusks, polychaetes	Birds

3. Results

We quantified parasitism in 7158 snails from five sites over 15 years. On average, we dissected 149 snails per site per year. Of those snails, 2311 snails were infected by trematodes.

We found six trematode species infecting snail populations in Sendai Bay both before and after the tsunami. The most abundant was *Cercaria batillariae* followed by *Cercaria hosoumininae* (Table 1). There were distinct behaviours of individual species after the tsunami. *Cercaria hosoumininae* was abundant at Nagazuraura before the tsunami, while its prevalence substantially decreased after the tsunami. A similar trend was observed at Katsugigaura and Torinoumi; *C. hosoumininae* was frequently observed before the tsunami but it was not observed after the tsunami. *Renicola* sp. 1 also nearly disappeared at Katsugigaura after the tsunami. On the other hand, the prevalence of *Acanthoparyphium* sp. 1 increased at Nagazuraura and Torinoumi after the tsunami.

The overall trematode prevalence was significantly reduced after the tsunami at the exposed sites ($df = 9$, $n = 4049$, $X^2 = 459.0$, $P < 0.01$) and the sheltered sites ($df = 9$, $n = 2260$, $X^2 = 582.4$, $P < 0.01$). The overall prevalences were relatively high in 2005 and 2006 but were dramatically lower in 2013 (Fig. 2A). The prevalence has decreased in 2013 and remained low at Torinoumi and Matsukawaura. High prevalences were occasionally recorded at Katsugigaura and Nagazuraura, but the prevalence otherwise remained low after the tsunami. The trematode species richness was higher before the tsunami than after the tsunami at the exposed sites ($F_{1,7,58} = 6.05$, $P < 0.05$). The richness decreased in 2013 and slowly increased after this severe reduction at the exposed sites (Fig. 2B). On the other hand, the trematode species richness was relatively stable over the study period at the sheltered sites ($F_{1,5,87} = 0.004$, $P = 0.95$, see Fig. 2B).

The nMDS analyses demonstrated that trematode community structure changed after the tsunami (Fig. 3). Trematode community structure was similar between 2005 and 2006, but largely fluctuated every year after the tsunami. The nMDS analyses showed that they have not transitioned into constant states and did not go back to the conditions before the tsunami.

4. Discussion

Trematode communities can provide insight into the damage and recovery of ecosystems after a major disturbance. Our baseline data of trematode community structure before the tsunami provides a test of the effects of the tsunami on the intertidal trematode communities. Our data suggest that the trematode prevalence and species richness in Sendai Bay were significantly reduced after the tsunami and that community structure has not recovered 8 years after the tsunami.

The comparison between the sites exposed to the tsunami and those sheltered from the tsunami enables us to evaluate how the tsunami affected the trematode community. Our results exhibited that the trematode prevalence decreased at both the exposed and sheltered sites after the tsunami (Fig. 2A) while the reduction of

the trematode species richness was observed only at the exposed sites (Fig. 2B). The tsunamis devastated a broad geographical range of coastal habitat and affected coastal organisms (Kanaya et al., 2012; Miura et al., 2012; Urabe et al., 2013; Miura and Kanaya, 2017). On the other hand, the damage of coastal organisms at the sheltered sites was limited compared with the exposed sites. This suggests that the observed difference in trematode parasitism between the exposed and sheltered sites is likely associated with the scale of the disturbance of coastal organisms that include the first and second intermediate hosts of the trematodes.

One of the major factors which reduced prevalence was probably the initial reduction of the populations of *B. attramentaria* at the sites exposed to the tsunami (Miura et al., 2012). While the pre-tsunami density of *B. attramentaria* often exceeded 100 m^{-2} , snails were absent in many of our quadrats after the tsunami (Miura et al., 2012, 2017) and trematodes were lost with the snails (Fig. 2A). While snails eventually recolonized (Miura et al., 2017), trematode prevalence remained low compared with before the tsunami (Fig. 2A and B). Oddly, the trematode prevalence and richness were relatively high in 2012. Most of the snails found in 2012 were large adult snails that had survived the tsunami (Miura et al., 2012). Since *B. attramentaria* is a long-lived species which can live for 6–10 years (Yamada, 1982) and trematodes can survive for several years within their first intermediate host (Curtis, 2003), the trematode parasitism in these surviving snails likely reflected pre-tsunami conditions. However, the prevalence reduced in 2013 (Fig. 2A and B) in response to the recruitment of uninfected snails (Miura et al., 2017). After 2013, immature snails comprised the majority of the populations and only became infected over time as they grew. The decline of *B. attramentaria* was also observed at the sheltered sites affected by subsidence (Mangokura) and human activity (Matsukawaura) (see Miura et al., 2017 for details). Therefore, the reduced trematode prevalence at the sheltered sites can also be explained by the decline of the host snail populations and the recruitment of uninfected snails.

Mollusks, polychaetes, crustaceans, and fishes serve as the second intermediate hosts of the trematodes infecting *B. attramentaria* (Table 1). These second intermediate hosts were also affected by the tsunami. For example, the populations of intertidal snails, *Batillaria multiformis*, *Cerithidea moerchii* and *Pirenella pupiformis* and the mud flat crab, *Chasmagnathus convexus*, were reduced or locally extirpated after the tsunami at several tide flats in Sendai Bay (Kanaya, G., Taru, M., Miura, O., Yuhara, T., Unagami, T., Tanaka, M., Mori, K., Aoki, M., Nakai, S., Itoh, H., Inoue, T., Suzuki, T., 2016. Impacts of the 2011 tsunami on tidal flat ecosystems: future perspectives for conservation of macrozoobenthic biodiversity. Proceedings of the 36th Annual Conference of the International Association for Impact Assessment, 11–14 May, 2016, Nagoya, Japan). Similarly, abundance of the intertidal clam, *Ruditapes philippinarum* decreased after the tsunami (Abe et al., 2017). Further, benthic polychaete worms and the fish community structures were also changed after the tsunami (Abe et al., 2015; Shoji and Morimoto, 2016). Since these intertidal and subtidal species are potential second intermediate hosts of the trematodes (Table 1),

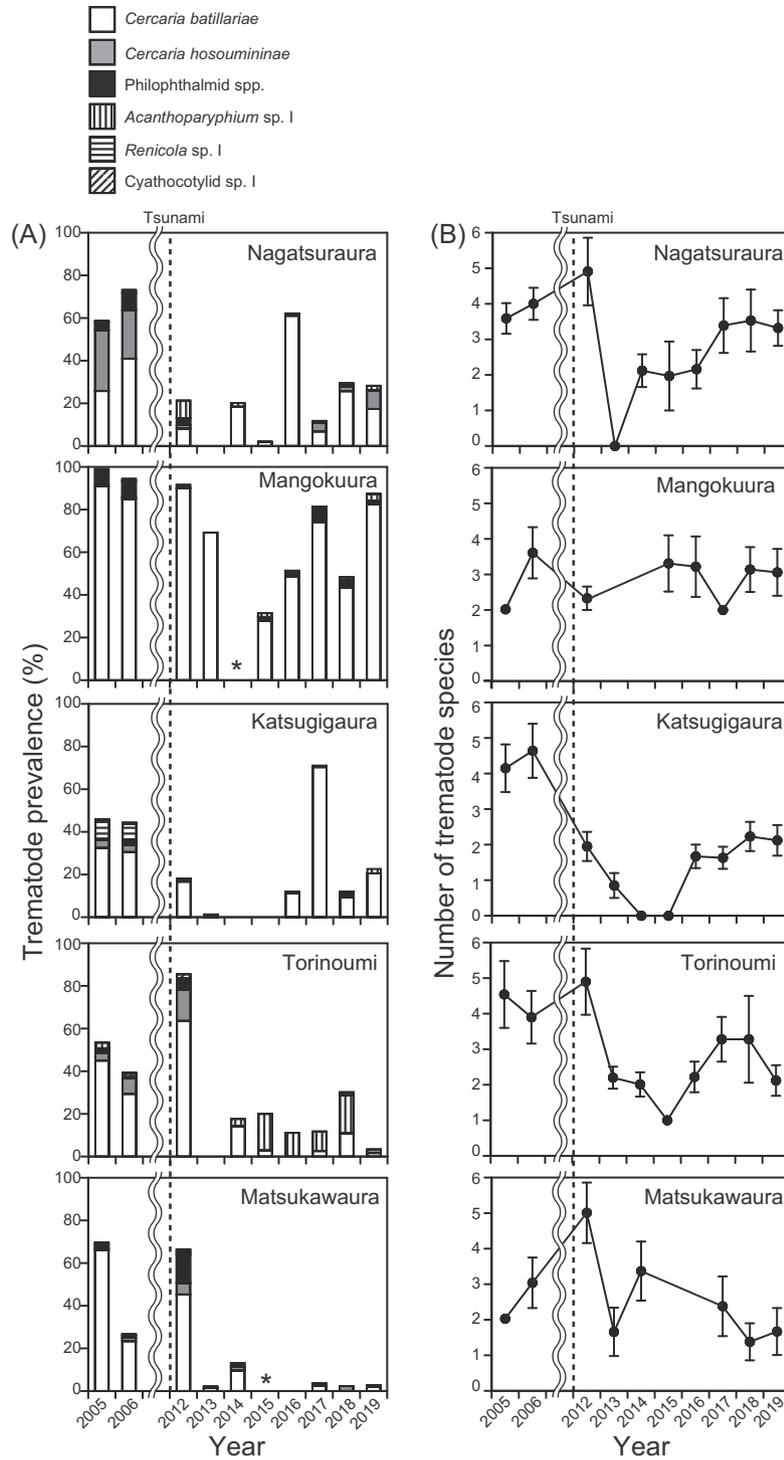


Fig. 2. The changes in the trematode community over the study period. (A) Trematode prevalences at the five study sites. Asterisks indicate that no host snails were found. (B) The rarefied trematode species richness across sampling years at the study sites. Error bars represent \pm S.D.

the overall declines and the changes in their community structures may account for some of the declines in richness and prevalence of trematodes in *B. attramentaria*. Indeed, the absence or reduced abundances of intermediate hosts may reduce transmission at local scales which could limit prevalences and species richness of trematodes (Huspeni et al., 2005; Torchin et al., 2015). On the other hand, there are likely to be smaller disturbances of second intermediate host populations at the sheltered sites than the exposed sites, which may partially explain the maintenance of trematode species richness at the sheltered sites.

Prevalence of *C. hosoumininae* substantially decreased at the exposed sites after the tsunami (Fig. 2A). In particular, this species has not been observed at Katsugigaura or Torinoumi after the tsunami. *Cercaria hosoumininae* uses crustaceans as second intermediate hosts (Table 1) and many crustacean species were reduced or temporally extirpated after the tsunami (Kanaya et al., 2012), suggesting the reduced availability of second intermediate hosts interrupted the local completion of trematode life cycles and caused the temporal reduction in *C. hosoumininae*. Both *Renicola* sp. I and *Acanthoparyphium* sp. I use mollusks and/or polychaetes as second

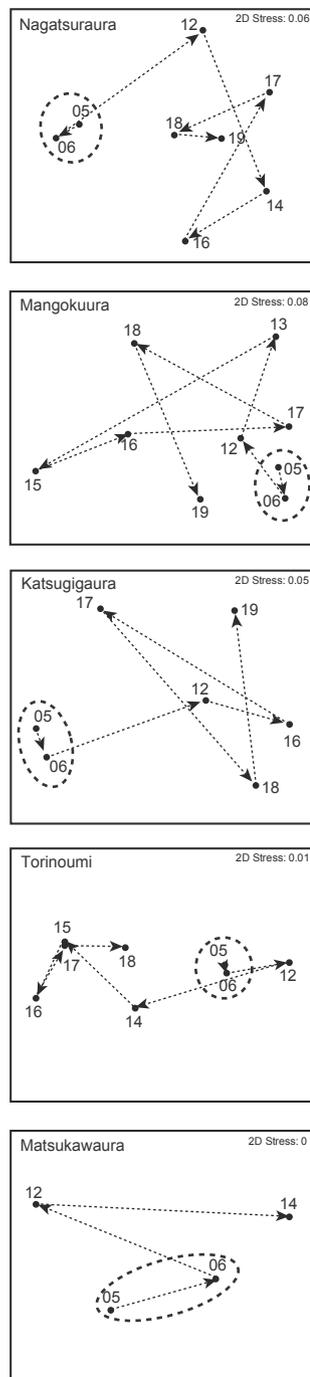


Fig. 3. Non-metric multidimensional scaling plot of the trematode community structure at the five study sites. The dotted circles show the community before the tsunami.

intermediate hosts (Table 1), but these two species exhibited contrasting demography after the tsunami. While *Renicola* sp. I decreased, *Acanthoparyphium* sp. I increased its abundance after the tsunami. Although they are known to use similar second intermediate hosts at a higher taxonomic level (Hechinger, 2007), their host usage pattern at the species level remains unclear. Future studies on their second intermediate hosts may provide a clue in understanding the distinct demography of *Renicola* sp. I and *Acanthoparyphium* sp. I after the tsunami.

Hechinger and Lafferty (2005) demonstrated that species richness and abundance of bird final hosts are positively correlated with trematodes in first intermediate hosts. Since the diversity and

abundance of intertidal macrobenthos were affected (Kanaya et al., 2012 and see above), shorebirds which feed on these macrobenthos may suffer from starvation and thus move to other tidal flats which were not affected by the tsunami. However, the results of shorebird monitoring demonstrate that there were no notable reductions in the abundance or species richness of shorebirds at three sites in Sendai Bay (Gamo Lagoon, Torinoumi, and Matsukawaura) between 2008 and 2012 (Kanaya et al., 2014), perhaps due to rapid recovery of opportunistic macrozoobenthos such as capitellid polychaetes and amphipods (Kanaya et al., 2012; Abe et al., 2015). This suggests that the bird final hosts may not account for the significant decrease in trematodes after the tsunami.

Trematode community structures were similar between 2005 and 2006 in each of the study sites but changed in 2012 after the tsunami and has fluctuated ever since (Fig. 3). Another study which examined the recovery of a trematode community after a hurricane disturbance found that it took 8 years to recover (Aguirre-Macedo et al., 2011). Our study suggests that after 8 years the trematode community has not fully recovered from the tsunami disturbance. Trematode communities are often positively associated with macrobenthic communities (Huspeni and Lafferty, 2004; Hechinger et al., 2007) and thus the recovery of the trematode community structure may require overall recovery of the macrobenthic communities. Abe et al. (2015) showed that the benthic polychaete community in Onagawa Bay substantially changed and entered a constant stage 3 years after the tsunami, while their community structure differed from the pre-tsunami community perhaps due to the change in sediment structure. This suggests that the trematode system will also stabilise at a species composition different from that before the tsunami. While trematode prevalence and species richness has gradually increased, trematode community structure has not fully recovered 8 years after the 2011 tsunami in Japan.

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