Title

Interspecific difference in the recovery of rocky intertidal zonation after the 2011 Great East Japan Earthquake

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Abstract

Both natural and anthropogenic disturbances have significant impacts on populations in terrestrial and marine habitats. Despite evidence that population recovery after large-scale disturbances in terrestrial habitats varies substantially among species depending on species traits and types of disturbance, little is known about interspecific differences in population recovery in marine habitats. In this study, we evaluated the course and status of recovery of the vertical distribution of nine intertidal sessile species over 6 years following the 2011 Great East Japan Earthquake. First, we characterized temporal changes in the vertical position of zonation as the spatial distribution, and total coverage as the local population size after the 2011 earthquake. Then, we evaluated the differences in successional status that explain interspecific differences in zonation recovery speed. Finally, we revealed that temporal changes in the vertical position and abundance after the earthquake differed according to species. The interspecific differences in the speed of recovery of zonation after 2014 were correlated with successional status, with later successional species having a delayed recovery rate. These results indicated that intertidal sessile assemblages continued to change 6 years after the large earthquake, suggesting that evaluations of the impacts of disturbances on assemblages and the course of community recovery require long periods of time.

Keywords

tsunami, subsidence, sessile species, benthic community, species trait

1. Introduction

Both natural and anthropogenic disturbances have significant impacts on populations of various organisms in terrestrial and marine habitats (Nyström, Folke, & Moberg, 2000; Sousa, 1984; Vörösmarty & Sahagian, 2000; White, 1985). Population recovery after a disturbance, which can be defined as the recovery of the abundance and distribution of a population to its natural state prior to the disturbance (Lotze, Coll, Magera, Ward-Paige, & Airoldi, 2011), varies substantially among species depending on species traits such as successional status in terrestrial habitats (Lavorel, McIntyre, Landsberg, & Forbes, 1997; Walker & del Moral, 2009) and the type of disturbance (e.g., Duarte, Conley, Carstensen, & Sánchez-Camacho, 2009; Kaiser et al., 2006; Worm et al. 2006). Although the type of disturbance and the species present are clearly distinct between terrestrial and marine habitats, successional status (i.e., niche position along a successional gradient) are common traits (Walker & del Moral, 2003). Therefore, successional status probably explains interspecific differences in population recovery in marine habitat.

The Great East Japan Earthquake with Mw 9.0 struck off the Pacific coast of the Tohoku region of Japan in 2011. The mega-earthquake caused a large tsunami with a maximum runup height of 40 meters and subsidence of several tens of centimeters throughout the entire Tohoku region (Lay & Kanamori, 2011; Mori, Takahashi, & 2011 Tohoku Earthquake Tsunami Joint Survey Group, 2012; Mori, Takahashi, Yasuda, & Yanagisawa, 2011; Tajima, Mori, & Kennett, 2013). Previous studies have suggested that earthquakes have considerable regional-scale impacts on populations of various marine benthos (Jaramillo et al., 2012; , Noda, Iwasaki, & Fukaya, 2016a,b; Seike, Shirai, & Kogure, 2013). This is because the tsunami and land level change caused by earthquakes can transport sessile organisms to unsuitable habitats (Castilla, 1988; Castilla, Manríquez,

& Camaño, 2010; Lomovasky, Firstater, Salazar, Mendo, & Iribarne, 2011; Noda et al., 2016a,b), affecting the survival and distribution of benthic species.

In rocky intertidal habitats, there is a notable vertical environmental gradient due to the effects of tides and waves (Connell, 1972; Raffaelli & Hawkins, 1996). In the upper intertidal zone, the immersion period is shorter than that in the lower intertidal zone, and physical conditions, such as temperatures and desiccation levels, are harsher (Helmuth & Hofmann, 2001; Menge & Branch, 2001). The magnitude of larval and propagule fluxes for sessile species is relatively low because these individuals are transported passively by waves (Bownes & McQuaid, 2006; Bownes & McQuaid 2009; Munroe & Noda, 2009; Raimondi, 1988). In comparison, in the lower intertidal zone, more species interactions occur, and predation pressure (e.g., Menge, 1978a,b; Paine, 1971) and species competition for space (e.g., Chapman, 1990; Connell, 1961a,b; Lubchenco, 1980) increase. Consequently, sessile species, such as barnacles, mussels, and macroalgae, are distributed within a vertical range of tens of centimeters; this is known as zonation and it is a common pattern worldwide (e.g., Dayton, 1971; Lewis, 1964; Menge, 1976; Stephenson & Stephenson, 1972).

The zonation of sessile species (i.e., their vertical position and abundance) along the Pacific coast of Tohoku region was altered by the Great East Japan Earthquake in 2011. This change in zonation was assumed to be the result of subsidence because the negative impacts of the tsunami on the abundance of sessile species was negligible (Iwasaki, Fukaya, & Noda, 2016; Iwasaki & Noda, 2018; Noda et al., 2016 a,b; see Supplemental Materials for details). Subsequently, zonation should be affected by the recruitment and mortality of sessile organisms. While previous studies have demonstrated that the dynamics of rocky intertidal zonation after the earthquake varied substantially

among species, the causes of these interspecific differences have not been examined (Noda et al. 2016a,b). Therefore, we hypothesized that interspecific differences in the speed of recovery of zonation can be explained by differences in the successional status of each species. Because early successional species exhibit greater recruitment of larvae or propagules and faster population growth after recruitment than late successional species (Farrell 1991), their zonation is likely to recover more quickly after an earthquake compared with later successional species.

In this paper, we report the course and status of recovery of the vertical distribution of nine rocky intertidal sessile species at 23 sites, located 150–160 km northwest of the epicenter of the 2011 Great East Japan Earthquake, over 6 years. First, we characterize temporal changes in the vertical position of zonation as the spatial distribution and total coverage as the local population size after the earthquake in 2011. Then, we evaluate the differences in successional status, a factor that could potentially explain interspecific differences in zonation recovery speed.

2. Materials and Methods

2.1 Study area

The study area was located along 30 km of coastline on the Sanriku Coast of Japan (Fig. 1). The study shores were 150–160 km north-northwest of the epicenter (38°06′12.0″N and 142°51′36.0″E) of the Great East Japan Earthquake, which caused large tsunami waves (run-up height, several to 30 m) and subsidence of 50–60 cm throughout the area (Lay & Kanamori, 2011; Noda et al., 2016a; Tajima et al., 2013). Low tide occurs during the day from April to September and at night from October to March. Dominant sessile species were the bivalves *Crassostrea gigas* and *Septifer virgatus*, the barnacles

116 *Chthamalus challengeri* and *Semibalanus cariosus*, and the perennial algae *Gloiopeltis*
117 *furcata*, *Analipus japonicus*, and *Hildenbrandia rubra*. Detailed information about biota
118 is provided in Okuda, Noda, Yamamoto, Ito, and Nakaoka (2004), Nakaoka, Ito,
119 Yamamoto, Okuda, and Noda (2006), and Fukaya, Okuda, Nakaoka, Hori, and Noda
120 (2010).
121
122 **2.2 Census design**
123 A hierarchical sampling design (Noda 2004) was applied for a census of five shores
124 separated by 2.6–7.9 km (Fig. 1). In July 2003, four or five sites within each shore were
125 chosen and two permanent rectangular plots were established within each site: control
126 plots and succession plots. Control plots were un-manipulated, and succession plots were
127 cleared of all organisms on the rock surfaces in July 2003 by burning with gas torches
128 and scratching with wire brushes. Each control and succession plot was 50 cm wide by
129 100 cm high, and the mean tidal level corresponded to the vertical midpoint.
130 Each control plot was extended 100 cm above in July 2011 (Fig. 2) because the
131 study area experienced subsidence due to the Great East Japan earthquake; vertical
132 subsidence was 50 cm at four shores (Myojin, Oura, Aragami, and Katagishi) and 60 cm
133 at Akahama (Noda et al. 2016a). Consequently, the vertical observation range for each
134 control plot was 200 cm after the earthquake. Here, it is noted that although uplift can
135 occur after subsidence, the effect of the uplift that occurred after the subsidence in the
136 study area was negligible due to the small range, which was about 2cm over the 6 years
137 following the earthquake (The Coordinating Committee for Earthquake Prediction, Japan,
138 2017).
139 Each control plot was divided vertically into subsections every 10 cm from the

upper edge; a plot had 10 and 20 subsections before and after the earthquake, respectively. In each subsection, 20 grid points were placed on the rock surface at 5-cm intervals in both the vertical and horizontal directions in each control plot. To estimate coverage as abundance, each sessile organism occupying a grid point was identified and recorded, and the total number of grid points for each sessile organism in each subsection was determined in each census. This census was carried out in July from 2004 to 2017 at low tide.

Each succession plot was divided vertically into subsections at 10-cm intervals; a plot had 10 subsections. In each subsection, the occurrence (i.e., presence or absence) of sessile organisms was recorded. This census was carried out each July from 2004 to 2010 at low tide.

2.3 Data analysis

To characterize the temporal changes in the vertical position of zonation as well as total coverage, the data from the entirety of the control plots (50 cm width × 200 cm height; Fig. 2 “raw zonation”) was used for two reasons. First, most of the vertical range of zonation of the focal species should be covered by the spatial scale of observation to reliably estimate its recovery rate. Second, sufficient numbers (~10) of species are required to perform statistical tests. The specific methods for characterizing temporal changes in vertical position and total coverage are described below in the section *Quantifying zonation*. To estimate the rate of population recovery after the earthquake, the zonation before the earthquake was defined as the zonation of the control plots in July 2011, which was shifted 50–60 cm upward (Fig. 2, “zonation of orange line”). Next, the

zonation after 2012 was compared with the zonation before the earthquake within the same tidal range; the data from the upper 50 cm before the earthquake and from the lower 50 cm after 2012 were not used for analysis (Fig. 2, “pink area”). The specific methods for the estimation are described below in the section *Recovery of zonation after the earthquake*. To estimate the species’ successional status, the data from the succession plots were used. The specific methods for estimation are described below in the section *Successional status*.

Species selection

We selected only common native species for analysis; invasive species (e.g., *Balanus grandula*) found in the study area were excluded. Additionally, species with a temporal mean value of coverage both before and after the earthquake lower than 0.5% were excluded. For species with low coverage, the vertical distribution and coverage can include large observation error, making it difficult to accurately estimate their zonation and/or coverage. Finally, species whose zonation changed between the tine of the earthquake (i.e., March 11, 2011) and July 2011 were excluded. To evaluate this, the mean zonation from 2003 to 2010 was compared with the zonation after the earthquake (the zonation in July 2011 was shifted 50 cm upward) by using the Kolmogorov–Smirnov test.

Based on the above criteria, nine sessile species were included in subsequent statistical analyses: four sessile animals (*Chthamalus challengeri*, *Hydroides ezoensis*, *Crassostrea gigas*, and *Septifer virgatus*) and five algae (*Condrus yendoi*, *Gloiopeltis furcate*, *Hildenbrandia rubra*, *Analipus japonicus*, and Corallinales spp.).

188 *Quantifying zonation*

189 Using the data accumulated from all control plots, the vertical distribution of each species
190 was obtained in each year as the mean coverage at the elevation of each of the subsection
191 relative to the mean tidal level. As a measure of the vertical position of zonation (i.e., the
192 spatial distribution of a species), the height corresponding to quartiles of the cumulative
193 frequency distribution (i.e., 25th, 50th, and 75th percentiles) along the tidal height was
194 calculated for each species in each year. In addition, as a measure of total coverage of the
195 local population, the sum of the mean coverage of each species was calculated in each
196 year for control plots.

197

198 *Recovery of zonation after the earthquake*

199 The recovery rate of zonation *t* years after the earthquake was calculated as the similarity
200 between the zonation before the earthquake and in each year after the earthquake (i.e.,
201 from 2012 to 2017) using Bray–Curtis index as follows:

202 $$\delta_{i,t} = 1 - \frac{\sum_h \left| N_{i,h}^{(before)} - N_{i,h,t} \right|}{\left(\sum_h N_{i,h}^{(before)} + \sum_h N_{i,h,t} \right)}.$$

203 Here, $N_{i,h}^{(before)}$ is the coverage before the earthquake in species *i* at subsection *h* (i.e.,
204 the zonation in July 2011 being shifted 50 cm upward) and $N_{i,h,t}$ is the coverage *t* years
205 after the earthquake in species *i* at subsection *h*. Bray–Curtis dissimilarity ranges from 0
206 to 1, and $\delta_{i,t}$ values near 1 indicate that zonation is highly similar before and after the
207 earthquake.

208

209 *Successional status*

210 As mentioned earlier, successional status is a species trait that may explain interspecific

differences in recovery rates. Successional status was estimated using Usher's succession index for species *i*, M_i, as follows (Usher 1970):

$$M_i = \frac{\sum_t y_i f_{i,t}}{F_{i,t}}.$$

Here, y_i is the years elapsed when 2004 is set to 1, $f_{i,t}$ is the occurrence frequency of species *i* in the year *t* (i.e., from 2004) in the succession plot, and $F_{i,t}$ is the sum of occurrence frequencies of species *i* from 2004 to 2010. M_i is larger if species *i* occurs in late successional stages.

Statistical analyses

The correlation between the recovery rates after the earthquake and successional status (i.e., Usher's succession index) was evaluated by Spearman's rank correlation coefficient. These statistical analyses were implemented in R 3.5.0 (R Development Core Team, 2018).

3. Results

3.1 Changes in zonation after the earthquake

Although all species exhibited upward shifts in their vertical positions of zonation after the earthquake, temporal patterns differed according to species (Figs. 3–4). In *C. challengeri*, *C. gigas*, *G. furcate*, and *A. japonicus*, the recovery of the vertical position was nearly complete within a few years after the earthquake. In others (i.e., *H. ezoensis*, *S. virgatus*, *C. yendoi*, *H. rubra*, and Corallinales spp.), the upward shifts were more gradual. The vertical positions of *S. virgatus* and *C. yendoi* varied among years.

Although the total coverage of most species increased immediately after the

earthquake, subsequent changes differed among species (Fig. 5). In *C. challengeri*, *C. gigas*, *G. furcate*, *A. japonicus*, and Corallinales spp., the total coverage increased in 2012 and fluctuated after 2013. In *H. ezoensis*, the total coverage increased. In *H. rubra* and *S. virgatus*, the total coverage decreased until 2015 and increased gradually thereafter.

3.2 Recovery of zonation after the earthquake

Temporal changes in recovery rates differed among species (Fig. 6). In *C. challengeri* and *H. ezoensis*, recovery rates increased by 2013 and then gradually decreased. In contrast, in *C. gigas*, *S. virgatus*, *C. yendoi*, *G. furcate*, and Corallinales spp., recovery rates decreased immediately after the earthquake and then increased slightly. In *H. rubra* and *A. japonicus*, recovery rates showed relatively little change during the study period.

3.3 Relationship between recovery rate and successional status

The correlations between the recovery rate and Usher's succession index were always negative (Fig. 7). The correlation tended to be stronger after 2014, but statistical significance was only obtained in 2016.

4. Discussion

Although the vertical position of zonation shifted upward after the earthquake in all species (Figs. 3–4), temporal changes in coverage differed among species (Fig. 5). Coverage increments accompanying the expansion of the vertical range of zonation, which were detected for *C. challengeri*, *H. ezoensis*, *C. gigas*, *G. frucata*, *A. japonicus*, and Corallinales spp., suggested that the increase in coverage by recruitment and

subsequent growth at the upper part of the zone was greater than the decline of coverage caused by death at the lower part of the zone. In contrast, the coverage decline accompanied by an upward shift of zonation, as detected for *H. rubra*, *S. virgatus*, and *C. yendoi*, suggests that the increment of coverage caused by recruitment and subsequent growth at the upper area was smaller than the decline of coverage caused by death at the lower area.

The negative correlation between the recovery rate and Usher's succession index tended to be stronger after 2014 (Fig. 7). While the recovery rates of early successional species did not change over time, those of intermediate and late species decreased, resulting in a negative correlation. Thus, the obtained results supported our prediction (i.e., pattern) that recovery rates of zonation are likely to be faster for early successional species than for late successional species. However, the impacts of the disturbance on intermediate and late successional species had a time lag, and the mechanism underlying the negative correlation may be complex.

The recovery rates of intermediate and late successional species were lower than those of early successional species, even in 2017 (Fig. 7). It is possible that intermediate and late successional species needed more time for population recovery after such a "giant" disturbance. The species with low recovery rates even in 2017, *C. gigas*, and *S. virgatus* (Fig. 7), act as facilitators for small sessile animals and mobile invertebrates by reducing abiotic stresses such as desiccation and biotic stresses such as predation (Witman 1985). Therefore, the low recovery rates of these species may be related to the community structure in intertidal assemblages.

Our results showed that temporal changes in coverage after subsidence were distinct among nine sessile species (Fig. 5). These findings are not consistent with

283 previous studies of similar taxonomic assemblages showing that the temporal change in
284 coverage after uplift did not differ among species; most species experienced immediate
285 mass mortality and subsequent declines in coverage after the Chilean earthquake in 1985
286 (Castilla, 1988; Durán & Castilla, 1989). This indicates that the temporal change in the
287 coverage of sessile species after an earthquake with subsidence is more complex and
288 variable than that with uplift. It might be caused by the more complex population
289 processes after subsidence than uplift. Shifts in sessile organisms beyond the lower limits
290 of zonation can cause transient increases in body growth by increasing the immersion
291 period (Raffaelli & Hawkins, 1996) and can often cause a gradual rise in mortality by
292 increasing the intensity of competition and consumption (Connell, 1972; Paine, 1974;
293 Underwood & Denley, 1984). Shifts beyond the upper limits of zonation can cause an
294 immediate increase in mortality by physical stress, including thermal stress and
295 desiccation (Helmuth, Mieszkowska, Moore, & Hawkins, 2006; Underwood & Denley,
296 1984). Furthermore, this difference in complexity in the temporal change of coverage
297 after the earthquake between cases of subsidence and uplift suggests that the same kind
298 of disturbance (i.e., an earthquake) can be followed by a highly different recovery process
299 depending on the conditions (i.e., direction of land level change).

300 Our results show that zonation of the sessile community had not recovered to the
301 pre-earthquake state 6 years after the earthquake; in most species, vertical distribution,
302 total coverage, and vertical position of zonation continued to fluctuate and their recovery
303 rates remained low (Figs. 3–6). By comparing the temporal change in zonation between
304 after subsidence following this earthquake and after uplift following the Chilean
305 earthquake in 1985, the time to recovery of zonation of the sessile community after the
306 land deformation and the difference depending on the direction of land deformation can

be predicted as follows. First, the recovery of zonation of the sessile community will require more than a few years either after subsidence or uplift. This is because the zonation of the sessile community did not recover to the pre-earthquake state 6 years after subsidence and 3 years after uplift, respectively. These findings suggest that the sessile community periodically experiences drastic changes in zonation and the recovery phase for several years in plate boundary areas where large earthquakes (>Mw 8.0) occur cyclically at intervals of decades or centuries (Ammon, Lay, & Simpson, 2010; Lay & Kanamori, 2011). Second, communities dominated by mussels will need more time to recover after subsidence (Rilov & Schiel, 2006) than after uplift. Mussels are apparently more vulnerable to increases in predation pressure caused by subsidence than to increases in physical stress caused by uplift. For example, *S. virgatus* decreased drastically by subsidence after this earthquake and did not recover in the 6 years following the earthquake (Fig 4). The mussel *Perumytilus purpuratus* did not decrease by uplift after the Chilean earthquake (Castilla, 1988, Durán & Castilla, 1989) but decreased drastically by an increase in the predator *Concholepas concholepas* caused by the exclusion of the top predator, humans (Durán & Castilla, 1989). These findings emphasize the importance of collecting information about the recovery process following an earthquake by long-term observation to reveal how the sessile community is determined and maintained at a large temporal scale.

Conclusion

We characterized the course and status of recovery of the vertical distribution of nine intertidal sessile species within 6 years after a mega-earthquake, the 2011 Great East Japan Earthquake. Temporal changes in vertical position and total coverage after the

earthquake differed according to species. Interspecific differences in the speed of recovery of zonation were correlated with successional status, with delayed recovery in later successional species. Based on our results, we obtained two major conclusions. First, successional status is likely to be an inherent species trait that is independent of habitat and can explain interspecific differences in population recovery. Second, intertidal sessile assemblages continued to change 6 years after the earthquake, suggesting the need for long-term monitoring to evaluate the impacts and the course of community recovery.

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584
585 **Figure legends**

586 **Fig. 1** Study site location. Five shores were chosen for the census of intertidal
587 organisms on the Sanriku coast along the Pacific coast of Japan. Cross mark represents
588 the epicenter of the Great East Japan Earthquake

589 **Fig. 2** Conceptual diagram of the vertical range between census and analytic region

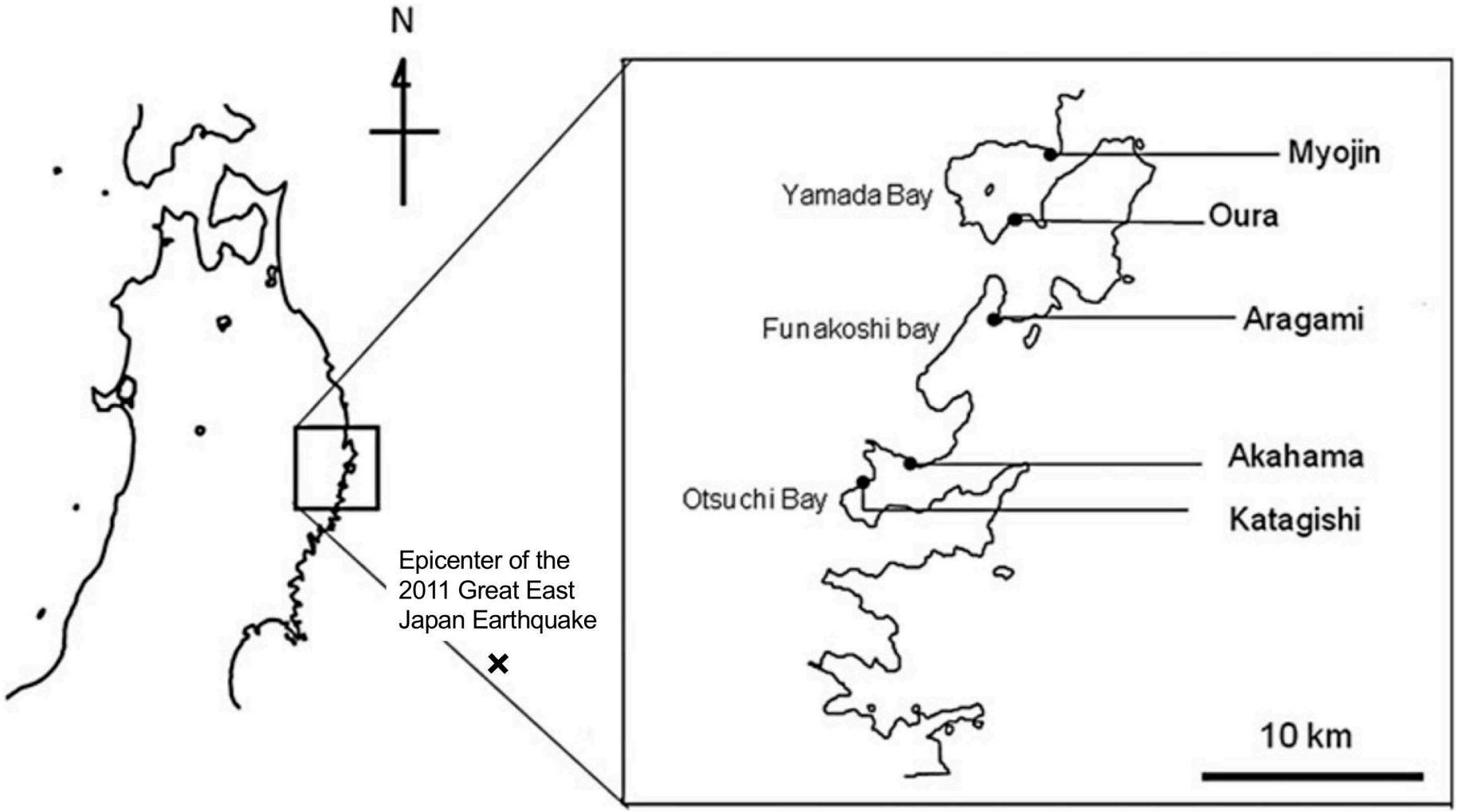
590 **Fig. 3** Course and status of the recovery of the vertical distribution of rocky intertidal
591 sessile organisms within 6 years after the mega-earthquake along the coast at locations
592 150–160 km north-northwest of the epicenter of the 2011 Great East Japan Earthquake

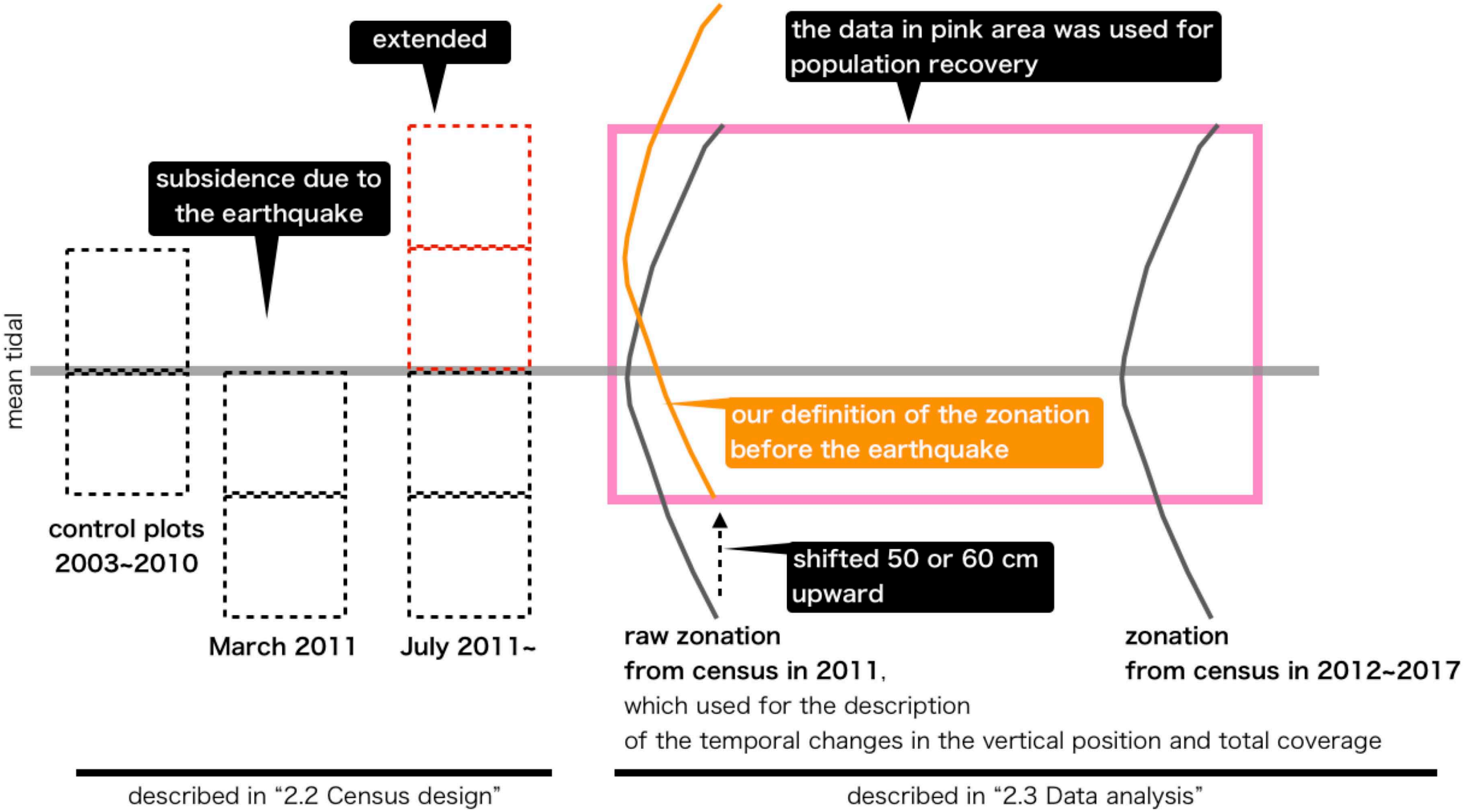
Fig. 4 Annual changes in the 25%, median, and 75% values in the cumulative frequency distribution of coverage in the vertical direction after the 2011 Great East Japan Earthquake

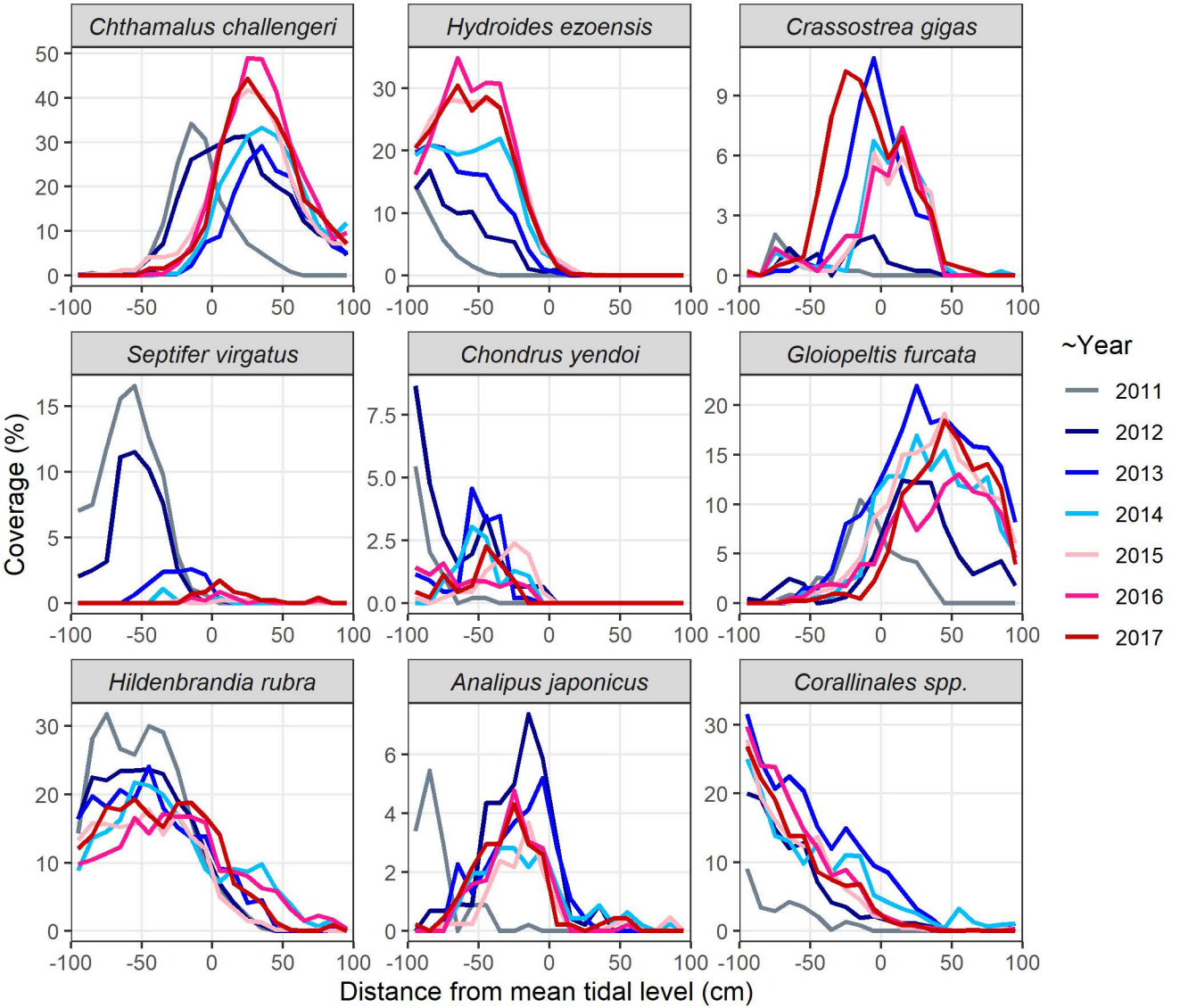
Fig. 5 Annual change in the total coverage of each species after the 2011 Great East Japan Earthquake

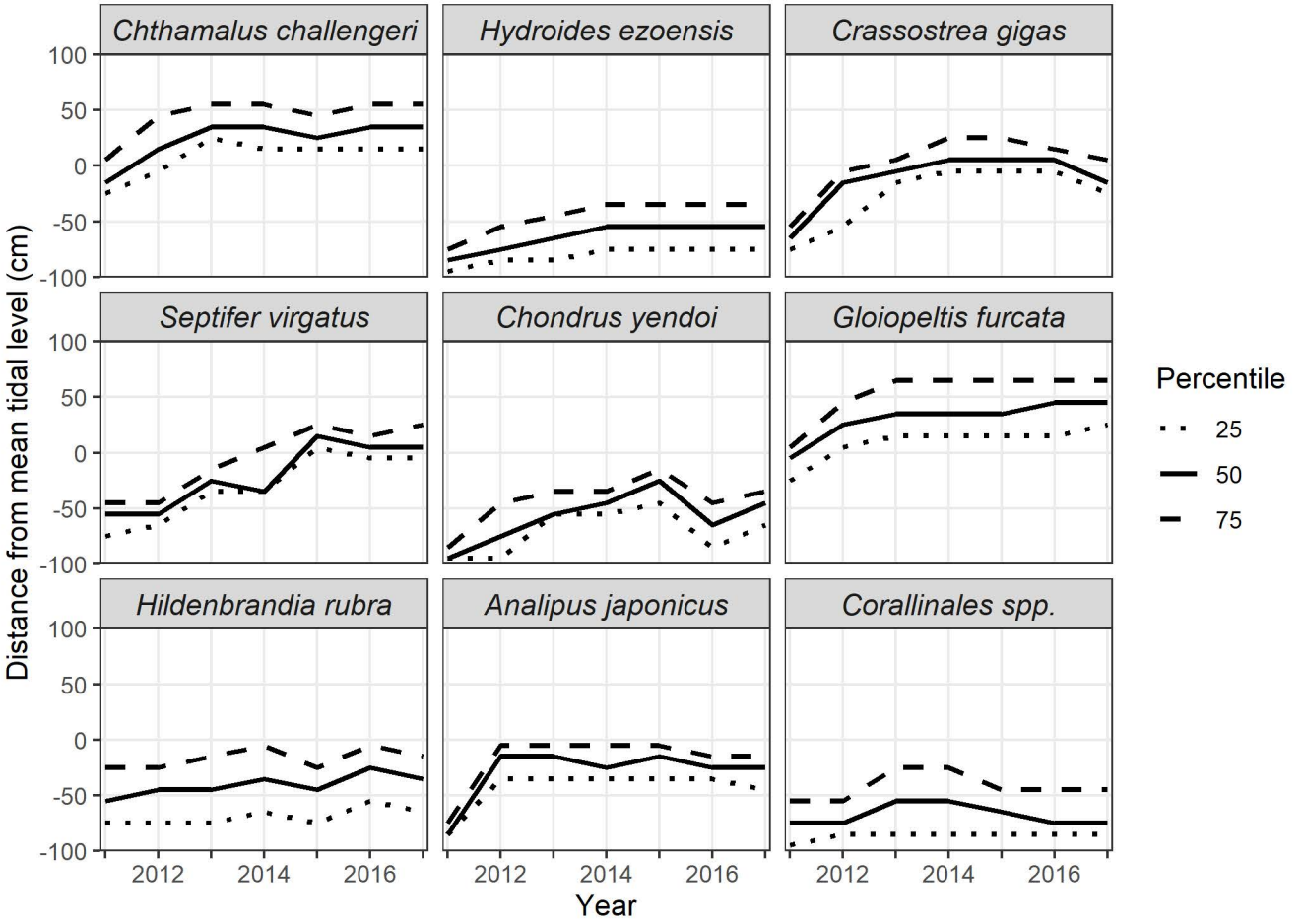
Fig. 6 Recovery rate for each species after the 2011 Great East Japan Earthquake

Fig. 7 Relationship between the recovery rate and Usher's succession index


N
Epicenter of the
2011 Great East
Japan Earthquake
Yamada Bay
Myojin
Oura
Funakoshi bay
Aragami
Akahama
Otsuchi Bay
Katagishi
10 km


extended
subsidence due to the earthquake
mean tidal
control plots 2003~2010
March 2011
July 2011~
the data in pink area was used for population recovery
our definition of the zonation before the earthquake
shifted 50 or 60 cm upward
raw zonation from census in 2011,
which used for the description of the temporal changes in the vertical position and total coverage
zonation from census in 2012~2017
described in “2.2 Census design”
described in “2.3 Data analysis”


Chthamalus challengeri
Hydroides ezoensis
Crassostrea gigas
Septifer virgatus
Chondrus yendoi
Gloiopeltis furcata
Hildenbrandia rubra
Analipus japonicus
Corallinales spp.
Coverage (%)
Distance from mean tidal level (cm)
~Year
2011
2012
2013
2014
2015
2016
2017


Chthamalus challengeri
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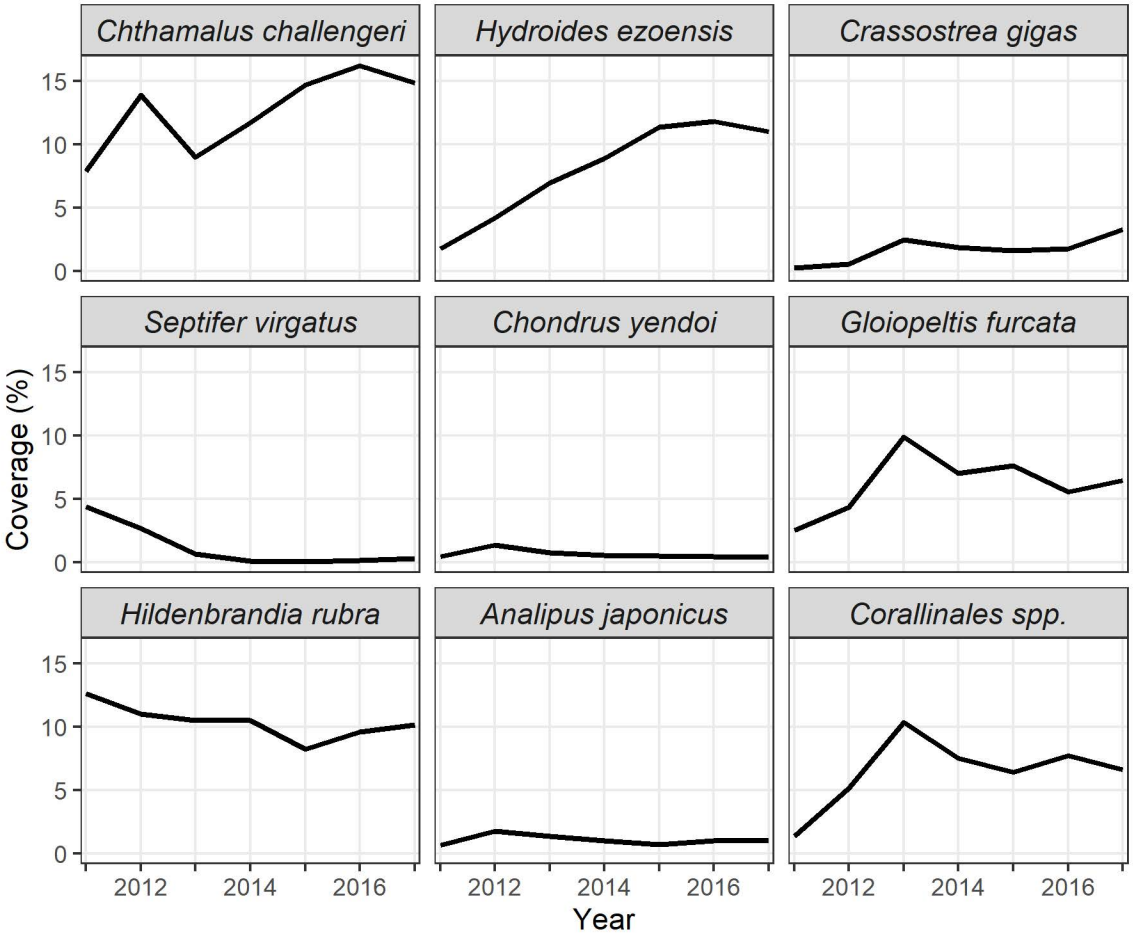
Crassostrea gigas
Septifer virgatus
Chondrus yendoi
Gloiopeltis furcata
Hildenbrandia rubra
Analipus japonicus
Corallinales spp.
Distance from mean tidal level (cm)
100
50
0
-50
-100
2012
2014
2016
Year
Percentile
25
50
75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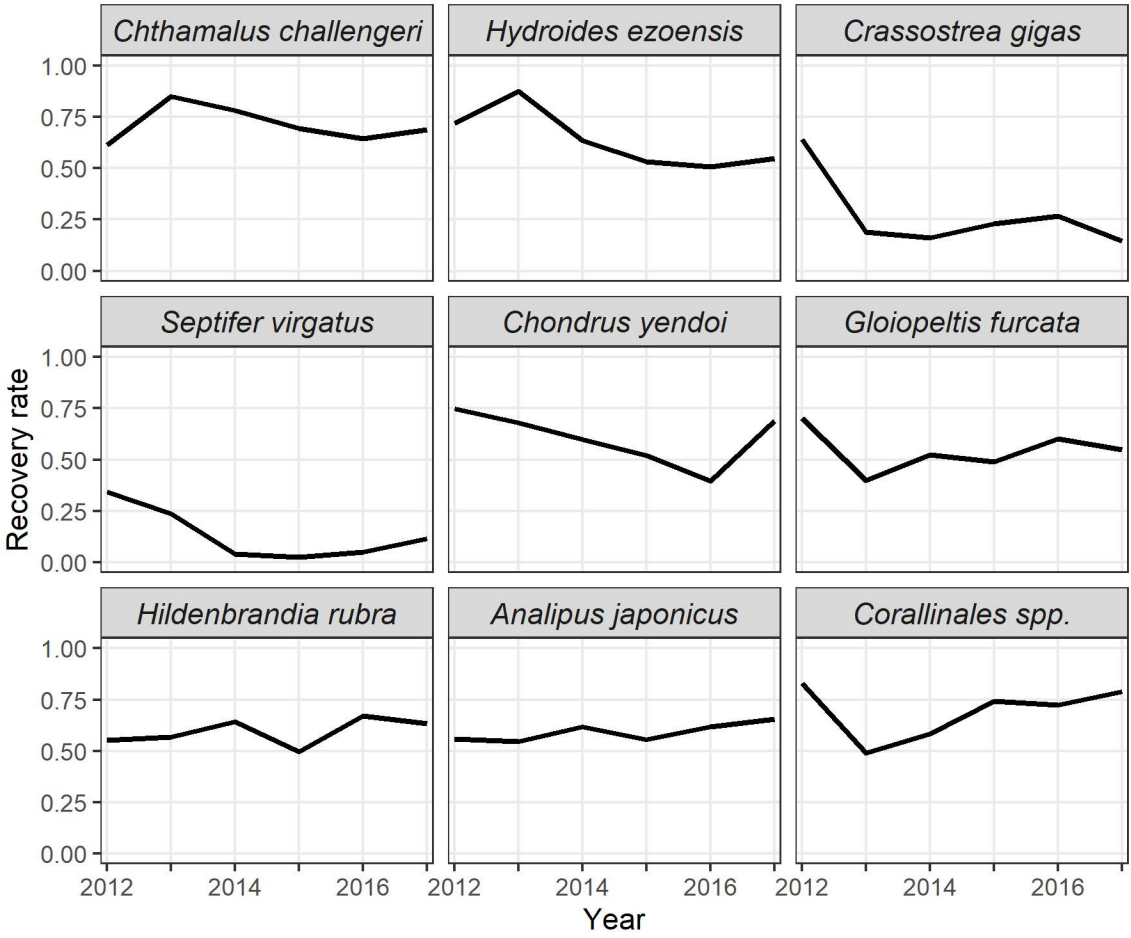
Crassostrea gigas
Septifer virgatus
Chondrus yendoi
Gloiopeltis furcata
Hildenbrandia rubra
Analipus japonicus
Corallinales spp.
Coverage (%)
0
5
10
15
2012
2014
2016
Year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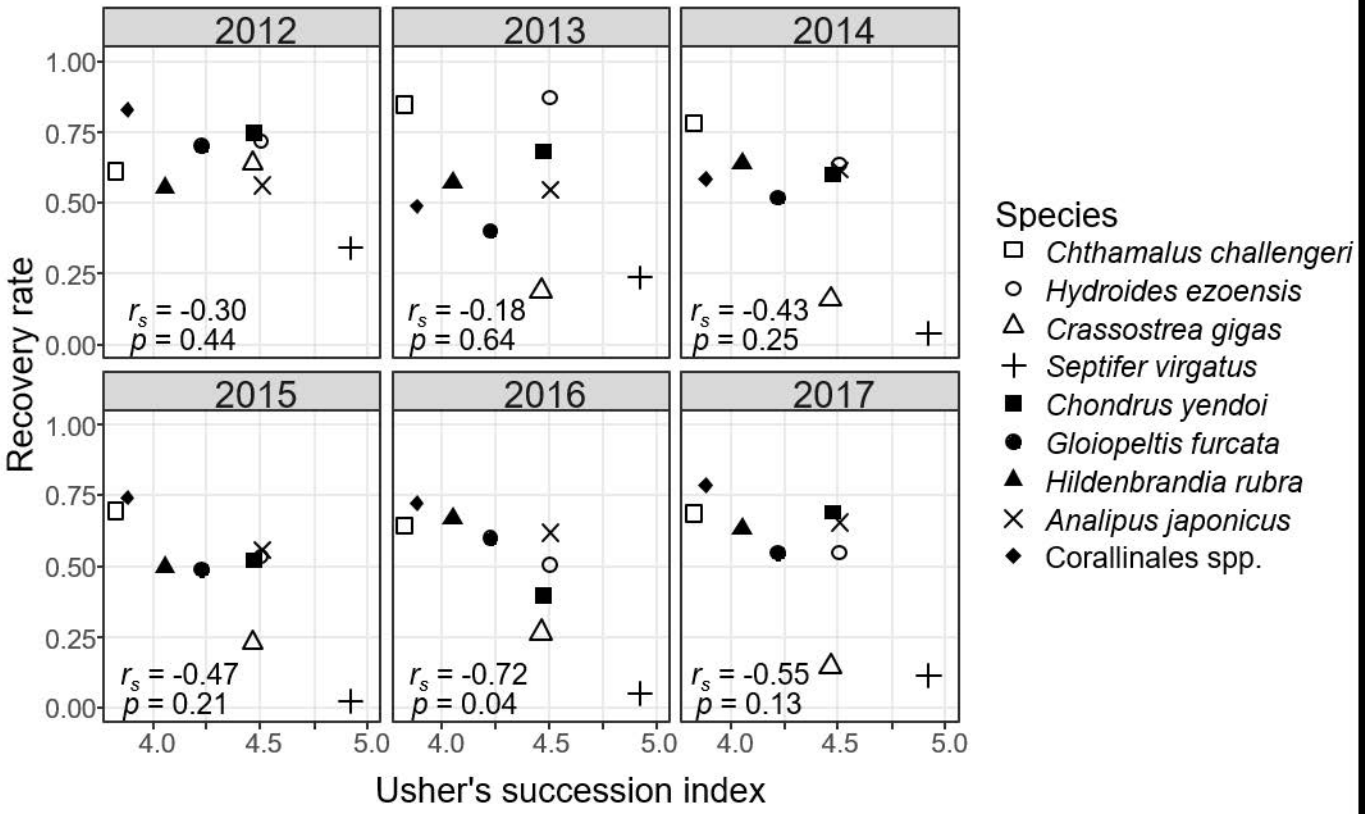
Crassostrea gigas
Septifer virgatus
Chondrus yendoi
Gloiopeltis furcata
Hildenbrandia rubra
Analipus japonicus
Corallinales spp.
Recovery rate
1.00
0.75
0.50
0.25
0.00
2012
2014
2016
Year


2012
2013
2014
2015
2016
2017
Recovery rate
1.00
0.75
0.50
0.25
0.00
r_s = -0.30
p = 0.44
r_s = -0.18
p = 0.64
r_s = -0.43
p = 0.25
r_s = -0.47
p = 0.21
r_s = -0.72
p = 0.04
r_s = -0.55
p = 0.13
4.0
4.5
5.0
Usher's succession index
Species
Chthamalus challengeri
Hydroides ezoensis
Crassostrea gigas
Septifer virgatus
Chondrus yendoi
Gloiopeltis furcata
Hildenbrandia rubra
Analipus japonicus
Corallinales spp.