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1 **Title**

2 Interspecific difference in the recovery of rocky intertidal zonation after the 2011 Great

3 East Japan Earthquake

4

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21

22   **Abstract**

23   Both natural and anthropogenic disturbances have significant impacts on populations in

24   terrestrial and marine habitats. Despite evidence that population recovery after large-scale

25   disturbances in terrestrial habitats varies substantially among species depending on

26   species traits and types of disturbance, little is known about interspecific differences in

27   population recovery in marine habitats. In this study, we evaluated the course and status

28   of recovery of the vertical distribution of nine intertidal sessile species over 6 years

29   following the 2011 Great East Japan Earthquake. First, we characterized temporal

30   changes in the vertical position of zonation as the spatial distribution, and total coverage

31   as the local population size after the 2011 earthquake. Then, we evaluated the differences

32   in successional status that explain interspecific differences in zonation recovery speed.

33   Finally, we revealed that temporal changes in the vertical position and abundance after

34   the earthquake differed according to species. The interspecific differences in the speed of

35   recovery of zonation after 2014 were correlated with successional status, with later

36   successional species having a delayed recovery rate. These results indicated that intertidal

37   sessile assemblages continued to change 6 years after the large earthquake, suggesting

38   that evaluations of the impacts of disturbances on assemblages and the course of

39   community recovery require long periods of time.

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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,

3

68   & Camaño, 2010; Lomovasky, Firstater, Salazar, Mendo, & Iribarne, 2011; Noda et al.,

69   2016a,b), affecting the survival and distribution of benthic species.

70   In rocky intertidal habitats, there is a notable vertical environmental gradient due

71   to the effects of tides and waves (Connell, 1972; Raffaelli & Hawkins, 1996). In the upper

72   intertidal zone, the immersion period is shorter than that in the lower intertidal zone, and

73   physical conditions, such as temperatures and desiccation levels, are harsher (Helmuth &

74   Hofmann, 2001; Menge & Branch, 2001). The magnitude of larval and propagule fluxes

75   for sessile species is relatively low because these individuals are transported passively by

76   waves (Bownes & McQuaid, 2006; Bownes & McQuaid 2009; Munroe & Noda, 2009;

77   Raimondi, 1988). In comparison, in the lower intertidal zone, more species interactions

78   occur, and predation pressure (e.g., Menge, 1978a,b; Paine, 1971) and species

79   competition for space (e.g., Chapman, 1990; Connell, 1961a,b; Lubchenco, 1980)

80   increase. Consequently, sessile species, such as barnacles, mussels, and macroalgae, are

81   distributed within a vertical range of tens of centimeters; this is known as zonation and it

82   is a common pattern worldwide (e.g., Dayton, 1971; Lewis, 1964; Menge, 1976;

83   Stephenson & Stephenson, 1972).

84   The zonation of sessile species (i.e., their vertical position and abundance) along

85   the Pacific coast of Tohoku region was altered by the Great East Japan Earthquake in

86   2011. This change in zonation was assumed to be the result of subsidence because the

87   negative impacts of the tsunami on the abundance of sessile species was negligible

88   (Iwasaki, Fukaya, & Noda, 2016; Iwasaki & Noda, 2018; Noda et al., 2016 a,b; see

89   Supplemental Materials for details). Subsequently, zonation should be affected by the

90   recruitment and mortality of sessile organisms. While previous studies have demonstrated

91   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

6

140   upper edge; a plot had 10 and 20 subsections before and after the earthquake, respectively.

141   In each subsection, 20 grid points were placed on the rock surface at 5-cm intervals in

142   both the vertical and horizontal directions in each control plot. To estimate coverage as

143   abundance, each sessile organism occupying a grid point was identified and recorded, and

144   the total number of grid points for each sessile organism in each subsection was

145   determined in each census. This census was carried out in July from 2004 to 2017 at low

146   tide.

147   Each succession plot was divided vertically into subsections at 10-cm intervals;

148   a plot had 10 subsections. In each subsection, the occurrence (i.e., presence or absence)

149   of sessile organisms was recorded. This census was carried out each July from 2004 to

150   2010 at low tide.

151

152

153   **2.3 Data analysis**

154   To characterize the temporal changes in the vertical position of zonation as well as total

155   coverage, the data from the entirety of the control plots (50 cm width $\times$ 200 cm height;

156   Fig. 2 "raw zonation") was used for two reasons. First, most of the vertical range of

157   zonation of the focal species should be covered by the spatial scale of observation to

158   reliably estimate its recovery rate. Second, sufficient numbers (~10) of species are

159   required to perform statistical tests. The specific methods for characterizing temporal

160   changes in vertical position and total coverage are described below in the section

161   *Quantifying zonation*. To estimate the rate of population recovery after the earthquake,

162   the zonation before the earthquake was defined as the zonation of the control plots in July

163   2011, which was shifted 50–60 cm upward (Fig. 2, "zonation of orange line"). Next, the

164 zonation after 2012 was compared with the zonation before the earthquake within the

165 same tidal range; the data from the upper 50 cm before the earthquake and from the lower

166 50 cm after 2012 were not used for analysis (Fig. 2, "pink area"). The specific methods

167 for the estimation are described below in the section *Recovery of zonation after the*

168 *earthquake*. To estimate the species' successional status, the data from the succession

169 plots were used. The specific methods for estimation are described below in the section

170 *Successional status*.

171

172 *Species selection*

173 We selected only common native species for analysis; invasive species (e.g., *Balanus*

174 *grandula*) found in the study area were excluded. Additionally, species with a temporal

175 mean value of coverage both before and after the earthquake lower than 0.5% were

176 excluded. For species with low coverage, the vertical distribution and coverage can

177 include large observation error, making it difficult to accurately estimate their zonation

178 and/or coverage. Finally, species whose zonation changed between the tine of the

179 earthquake (i.e., March 11, 2011) and July 2011 were excluded. To evaluate this, the

180 mean zonation from 2003 to 2010 was compared with the zonation after the earthquake

181 (the zonation in July 2011 was shifted 50 cm upward) by using the Kolmogorov–Smirnov

182 test.

183 Based on the above criteria, nine sessile species were included in subsequent

184 statistical analyses: four sessile animals (*Chthamalus challengeri*, *Hydroides ezoensis*,

185 *Crassostrea gigas*, and *Septifer virgatus*) and five algae (*Condrus yendoi*, *Gloiopeltis*

186 *furcate*, *Hildenbrandia rubra*, *Analipus japonicus*, and Corallinales spp.).

187

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

211   differences in recovery rates. Successional status was estimated using Usher's succession

212   index for species i, M_i, as follows (Usher 1970):

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

214   Here, y_i is the years elapsed when 2004 is set to 1, $f_{i,t}$ is the occurrence frequency of

215   species i in the year t (i.e., from 2004) in the succession plot, and $F_{i,t}$ is the sum of

216   occurrence frequencies of species i from 2004 to 2010. M_i is larger if species i occurs in

217   late successional stages.

218

219   *Statistical analyses*

220   The correlation between the recovery rates after the earthquake and successional status

221   (i.e., Usher's succession index) was evaluated by Spearman's rank correlation coefficient.

222   These statistical analyses were implemented in R 3.5.0 (R Development Core Team,

223   2018).

224

225

226   **3. Results**

227   **3.1 Changes in zonation after the earthquake**

228   Although all species exhibited upward shifts in their vertical positions of zonation after

229   the earthquake, temporal patterns differed according to species (Figs. 3–4). In *C.*

230   *challengeri*, *C. gigas*, *G. furcate*, and *A. japonicus*, the recovery of the vertical position

231   was nearly complete within a few years after the earthquake. In others (i.e., *H. ezoensis*,

232   *S. virgatus*, *C. yendoi*, *H. rubra*, and Corallinales spp.), the upward shifts were more

233   gradual. The vertical positions of *S. virgatus* and *C. yendoi* varied among years.

234   Although the total coverage of most species increased immediately after the

10

235   earthquake, subsequent changes differed among species (Fig. 5). In *C. challengeri*, *C.*

236   *gigas*, *G. furcate*, *A. japonicus*, and Corallinales spp., the total coverage increased in 2012

237   and fluctuated after 2013. In *H. ezoensis*, the total coverage increased. In *H. rubra* and *S.*

238   *virgatus*, the total coverage decreased until 2015 and increased gradually thereafter.

239

240   **3.2 Recovery of zonation after the earthquake**

241   Temporal changes in recovery rates differed among species (Fig. 6). In *C. challengeri*

242   and *H. ezoensis*, recovery rates increased by 2013 and then gradually decreased. In

243   contrast, in *C. gigas*, *S. virgatus*, *C. yendoi*, *G. furcate*, and Corallinales spp., recovery

244   rates decreased immediately after the earthquake and then increased slightly. In *H. rubra*

245   and *A. japonicus*, recovery rates showed relatively little change during the study period.

246

247   **3.3 Relationship between recovery rate and successional status**

248   The correlations between the recovery rate and Usher's succession index were always

249   negative (Fig. 7). The correlation tended to be stronger after 2014, but statistical

250   significance was only obtained in 2016.

251

252

253   **4. Discussion**

254   Although the vertical position of zonation shifted upward after the earthquake in all

255   species (Figs. 3–4), temporal changes in coverage differed among species (Fig. 5).

256   Coverage increments accompanying the expansion of the vertical range of zonation,

257   which were detected for *C. challengeri*, *H. ezoensis*, *C. gigas*, *G. frucata*, *A. japonicus*,

258   and Corallinales spp., suggested that the increase in coverage by recruitment and

11

259　subsequent growth at the upper part of the zone was greater than the decline of coverage

260　caused by death at the lower part of the zone. In contrast, the coverage decline

261　accompanied by an upward shift of zonation, as detected for *H. rubra*, *S. virgatus,* and *C.*

262　*yendoi*, suggests that the increment of coverage caused by recruitment and subsequent

263　growth at the upper area was smaller than the decline of coverage caused by death at the

264　lower area.

265　　　　The negative correlation between the recovery rate and Usher's succession index

266　tended to be stronger after 2014 (Fig. 7). While the recovery rates of early successional

267　species did not change over time, those of intermediate and late species decreased,

268　resulting in a negative correlation. Thus, the obtained results supported our prediction

269　(i.e., pattern) that recovery rates of zonation are likely to be faster for early successional

270　species than for late successional species. However, the impacts of the disturbance on

271　intermediate and late successional species had a time lag, and the mechanism underlying

272　the negative correlation may be complex.

273　　　　The recovery rates of intermediate and late successional species were lower than

274　those of early successional species, even in 2017 (Fig. 7). It is possible that intermediate

275　and late successional species needed more time for population recovery after such a "giant"

276　disturbance. The species with low recovery rates even in 2017, *C. gigas*, and *S. virgatus*

277　(Fig. 7), act as facilitators for small sessile animals and mobile invertebrates by reducing

278　abiotic stresses such as desiccation and biotic stresses such as predation (Witman 1985).

279　Therefore, the low recovery rates of these species may be related to the community

280　structure in intertidal assemblages.

281　　　　Our results showed that temporal changes in coverage after subsidence were

282　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

307 be predicted as follows. First, the recovery of zonation of the sessile community will

308 require more than a few years either after subsidence or uplift. This is because the

309 zonation of the sessile community did not recover to the pre-earthquake state 6 years after

310 subsidence and 3 years after uplift, respectively. These findings suggest that the sessile

311 community periodically experiences drastic changes in zonation and the recovery phase

312 for several years in plate boundary areas where large earthquakes (>Mw 8.0) occur

313 cyclically at intervals of decades or centuries (Ammon, Lay, & Simpson, 2010; Lay &

314 Kanamori, 2011). Second, communities dominated by mussels will need more time to

315 recover after subsidence (Rilov & Schiel, 2006) than after uplift. Mussels are apparently

316 more vulnerable to increases in predation pressure caused by subsidence than to increases

317 in physical stress caused by uplift. For example, *S. virgatus* decreased drastically by

318 subsidence after this earthquake and did not recover in the 6 years following the

319 earthquake (Fig 4). The mussel *Perumytilus purpuratus* did not decrease by uplift after

320 the Chilean earthquake (Castilla, 1988, Durán & Castilla, 1989) but decreased drastically

321 by an increase in the predator *Concholepas concholepas* caused by the exclusion of the

322 top predator, humans (Durán & Castilla, 1989). These findings emphasize the importance

323 of collecting information about the recovery process following an earthquake by long-

324 term observation to reveal how the sessile community is determined and maintained at a

325 large temporal scale.

326

327 **Conclusion**

328 We characterized the course and status of recovery of the vertical distribution of nine

329 intertidal sessile species within 6 years after a mega-earthquake, the 2011 Great East

330 Japan Earthquake. Temporal changes in vertical position and total coverage after the

331   earthquake differed according to species. Interspecific differences in the speed of

332   recovery of zonation were correlated with successional status, with delayed recovery in

333   later successional species. Based on our results, we obtained two major conclusions. First,

334   successional status is likely to be an inherent species trait that is independent of habitat

335   and can explain interspecific differences in population recovery. Second, intertidal sessile

336   assemblages continued to change 6 years after the earthquake, suggesting the need for

337   long-term monitoring to evaluate the impacts and the course of community recovery.

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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

593 **Fig. 4** Annual changes in the 25%, median, and 75% values in the cumulative frequency

594 distribution of coverage in the vertical direction after the 2011 Great East Japan

595 Earthquake

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

597 Japan Earthquake

598 **Fig. 6** Recovery rate for each species after the 2011 Great East Japan Earthquake
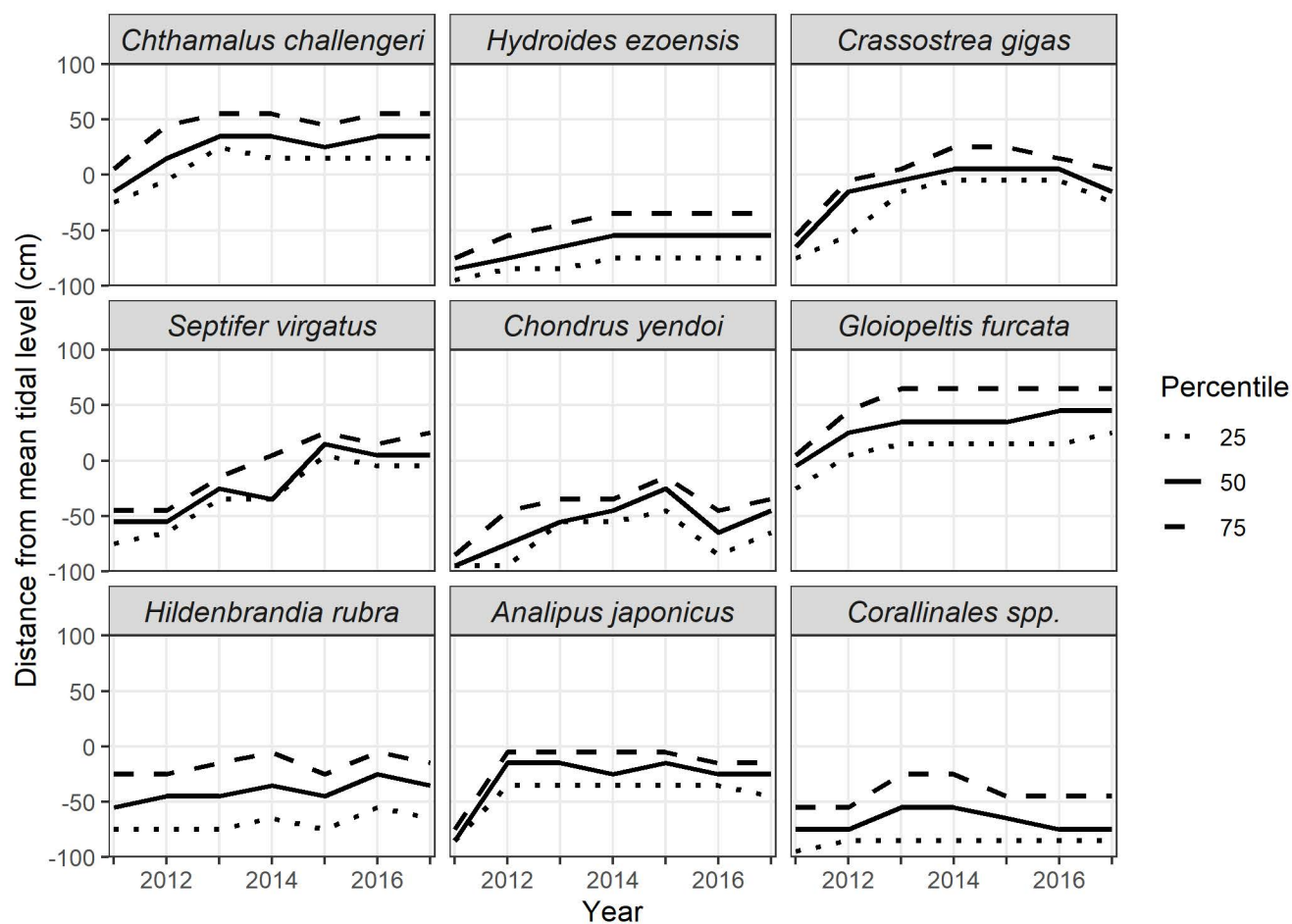
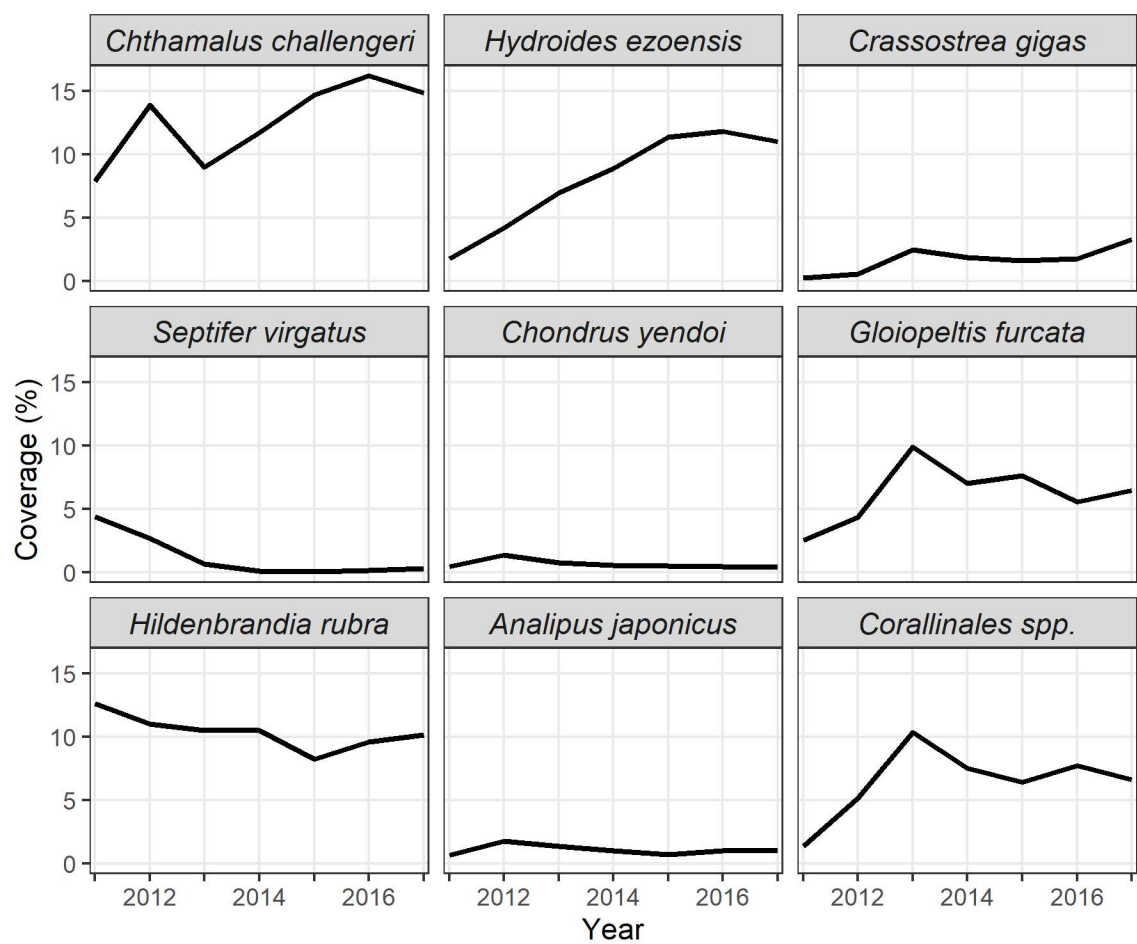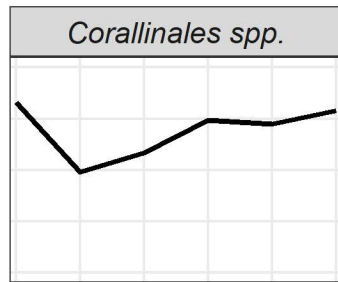599 **Fig. 7** Relationship between the recovery rate and Usher's succession index

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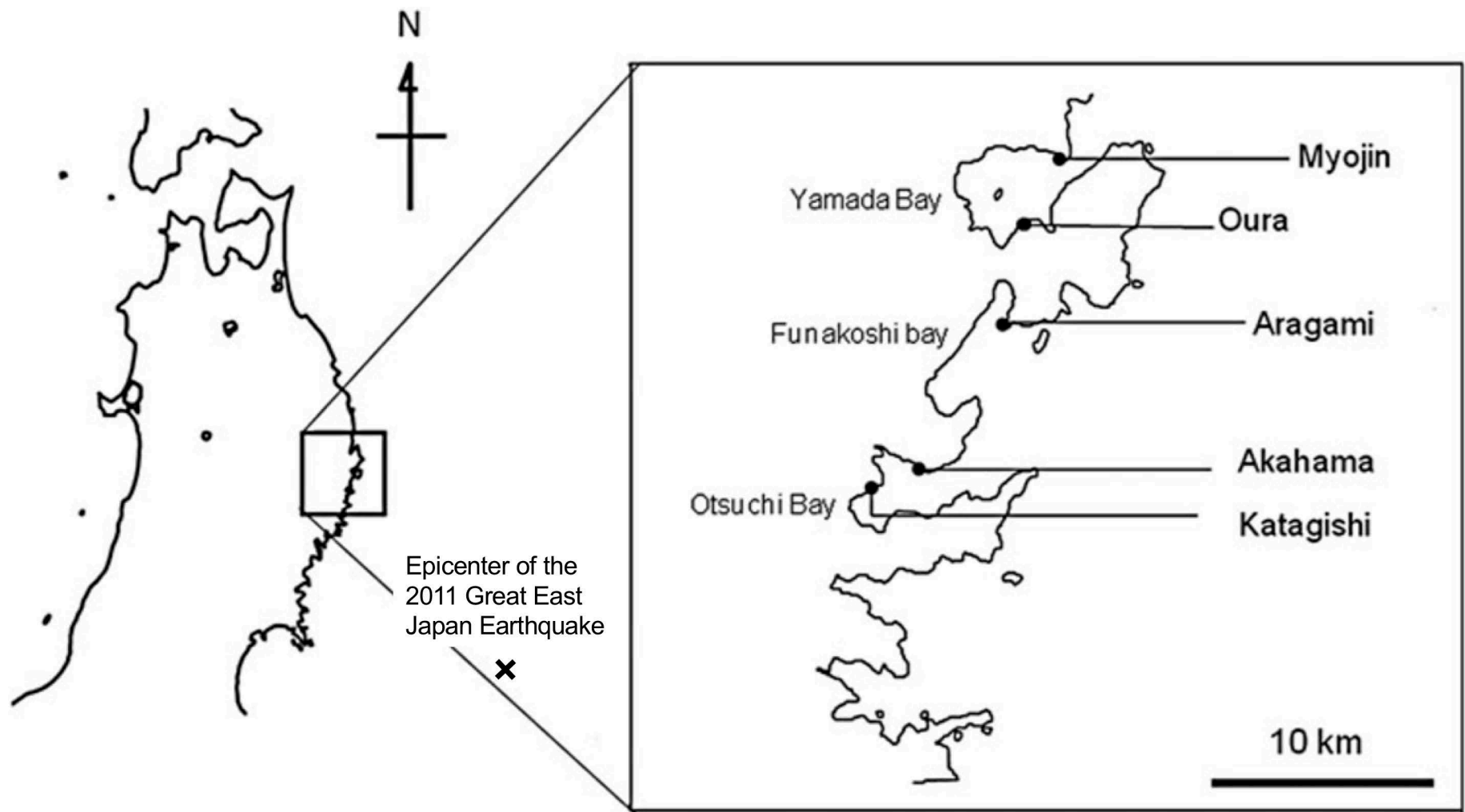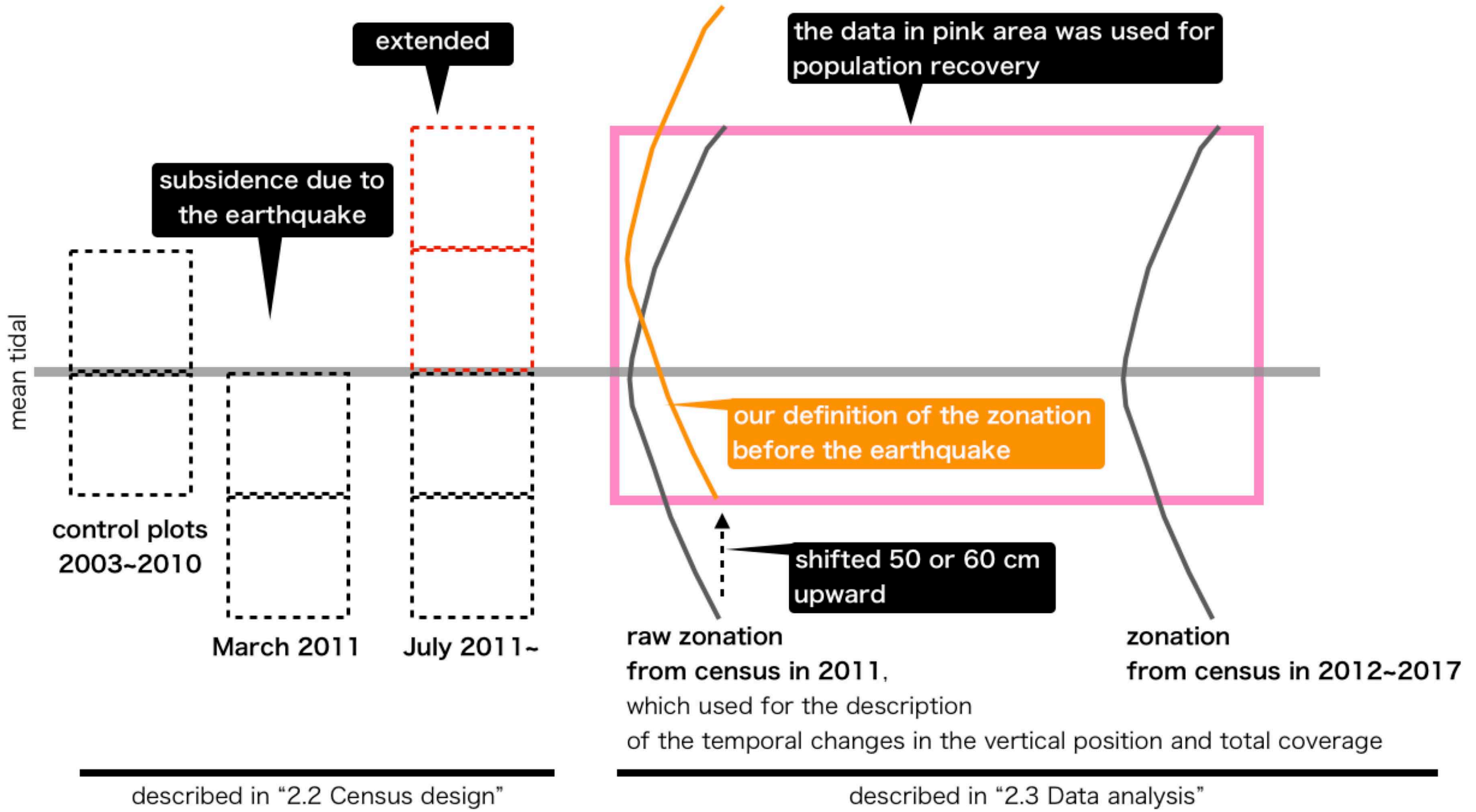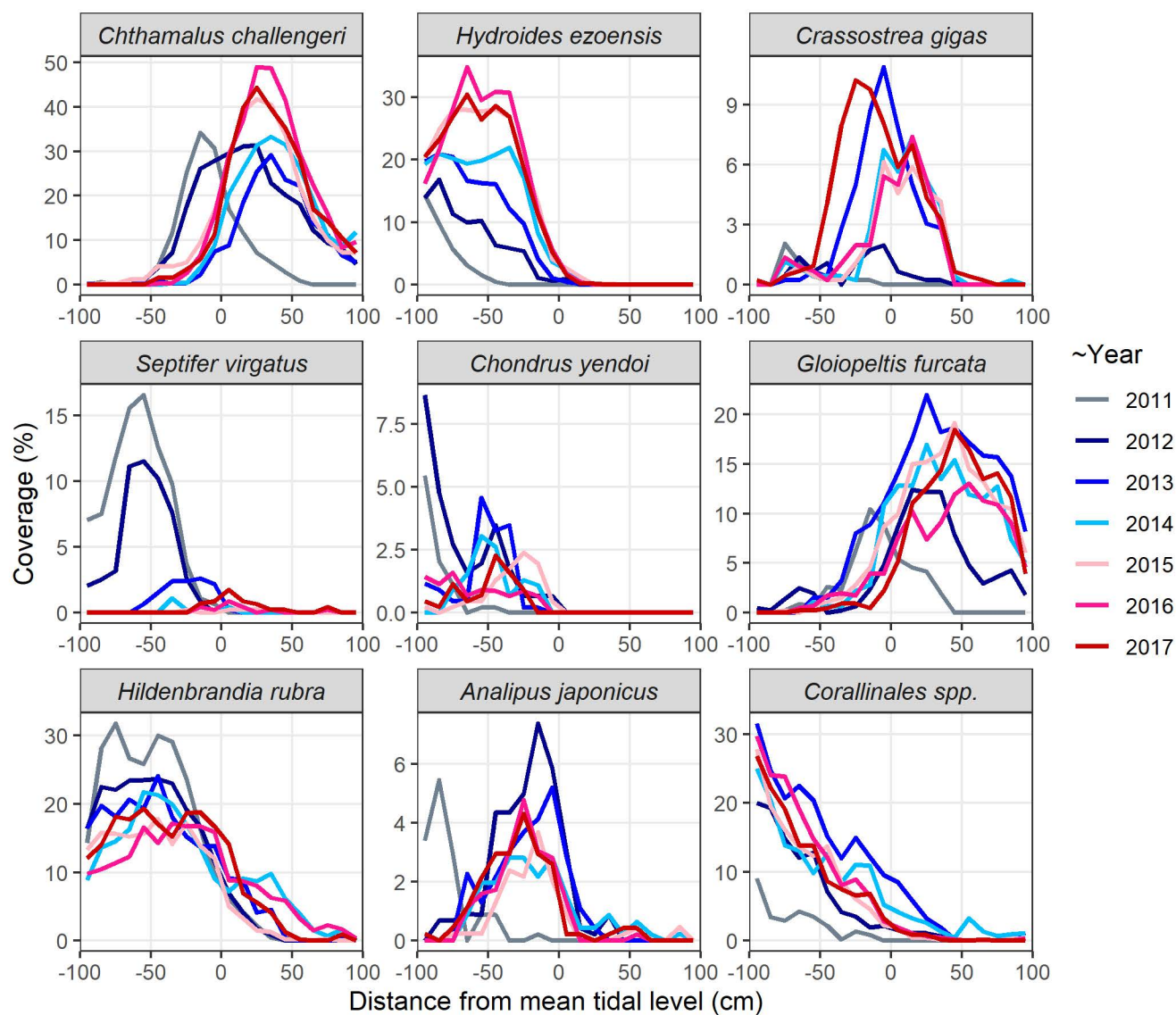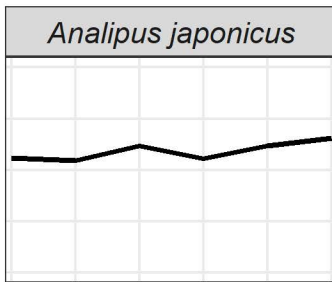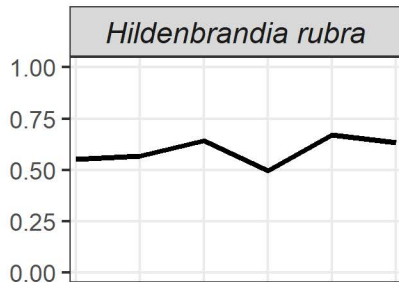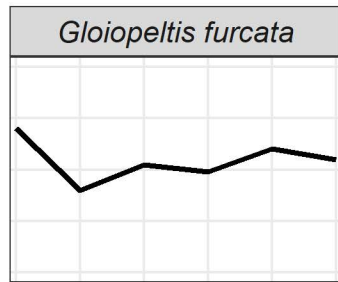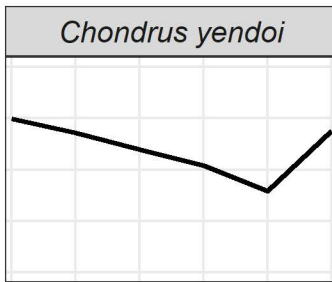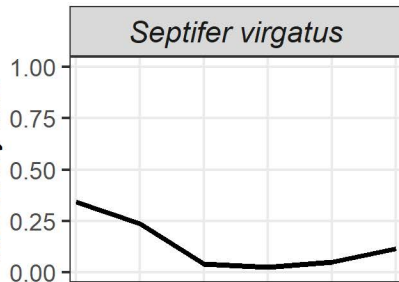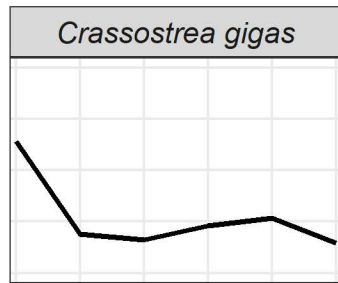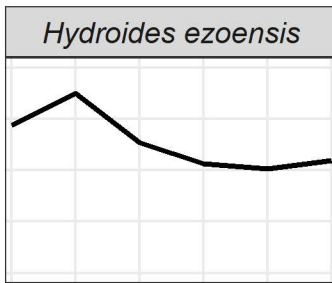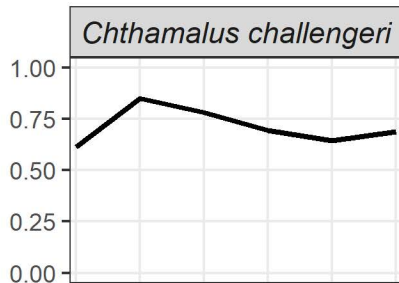
N

Myojin

Yamada Bay

Oura

Funakoshi bay

Aragami

Akahama

Otsuchi Bay

Katagishi

Epicenter of the
2011 Great East
Japan Earthquake

✕

10 km
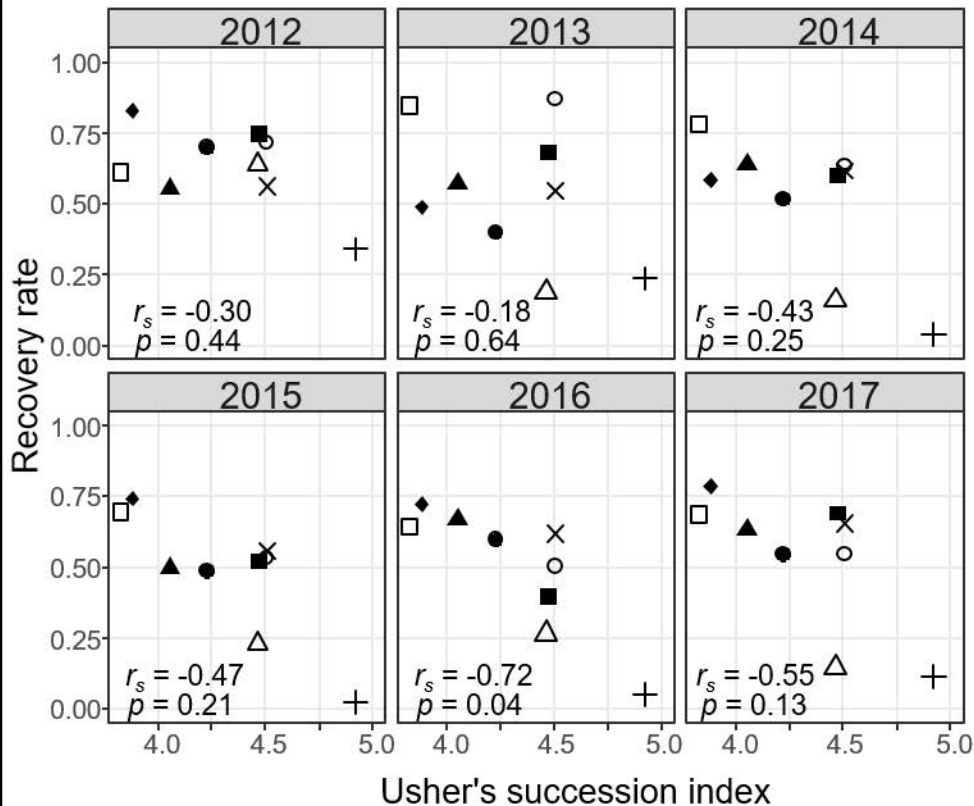
Coverage (%) versus Distance from mean tidal level (cm) for nine species across years (2011–2017): *Chthamalus challengeri*, *Hydroides ezoensis*, *Crassostrea gigas*, *Septifer virgatus*, *Chondrus yendoi*, *Gloiopeltis furcata*, *Hildenbrandia rubra*, *Analipus japonicus*, *Corallinales spp.*

~Year
— 2011
— 2012
— 2013
— 2014
— 2015
— 2016
— 2017