Coastal Marine Science 40(2): 35–43, 2017

Influence of the 2011 Tohoku Earthquake on population dynamics of a rocky intertidal barnacle: cause and consequence of alteration in larval recruitment

Takashi Noda*[1], Masayuki Sakaguchi[2] Aiko Iwasaki[1,2] and Keiichi Fukaya[3]

[1] Faculty of Environmental Earth Science, Hokkaido University, North 10 West 5, Kita-ku, Sapporo, Hokkaido 080–0610, Japan
[2] Graduate School of Environmental Science, Hokkaido University, North 10 West 5, Kita-ku, Sapporo, Hokkaido 080–0610, Japan
[3] The Institute of Statistical Mathematics, 10–3 Midori-cho, Tachikawa, Tokyo 190–8562, Japan
** E-mail: noda@ees.hokudai.ac.jp*

Received 2 December 2015; Accepted 31 March 2016

Abstract — By analyzing data obtained from 23 plots on five shores along the Pacific coast of Japan over 7 years, we explored the influence of the 2011 Tohoku Earthquake on the population dynamics of a rocky intertidal barnacle, *Chthamalus challengeri*. We addressed the following three questions. (1) At local and intermediate scales, how did the spatial patterns of larval recruitment change after the earthquake? (2) At broader spatial scales encompassing the entire meta-population, did larval recruitment change with the alteration of stock size after the earthquake? (3) How did the relative importance of larval recruitment as a determinant of local population growth rate change after the earthquake? The results demonstrated that while the spatial pattern of *C. challengeri* larval recruitment was only slightly modified by the 2011 earthquake, the population dynamics were significantly changed immediately (1–2 years) after the earthquake at two contrasting spatial scales. At a broad spatial scale encompassing several bays, the population size increased, consequently enhancing recruitment intensity, whereas at the local scale, the dependence of local population growth rate on larval recruitment increased. The former finding contradicts a widely accepted assumption that severe physical disturbances occurring at a broad spatial scale heavily impact natural populations.

Key words: barnacle, population dynamics, recruitment, rocky intertidal, Sanriku, subsidence, tsunami

Introduction

Most marine benthos exhibit complex life cycles that include pelagic larval stages and benthic stages linked by recruitment (Todd 1998). The transition between the two life stages can therefore be crucial to the population dynamics of these organisms (Thorson 1950). The structure and size of benthic populations are often governed by larval recruitment variability at the local scale (Gaines and Roughgarden 1985), whereas at broader spatial scales encompassing an entire meta-population, the larval recruitment should depend on stock size via regional reproductive output (Hughes et al. 2000). At local and intermediate scales the recruitment variability is strongly influenced by passive transport processes that depend on coastal topography and hydrodynamic features of coastal currents (reviewed by Shanks 1995).

The 2011 Tohoku Earthquake (M_w 9.0 on the moment magnitude scale), which caused a large tsunami and subsidence of 35–70 cm over the entire Tohoku region in Japan (Okada 2011), may have greatly impacted populations of marine benthos, and especially of rocky intertidal sessile organisms. Extremely strong wave action and scouring by floating wreckage associated with a tsunami can cause mass mortality of rocky intertidal sessile organisms. In addition, subsidence can transport rocky intertidal sessile organisms below their normal vertical ranges, where conditions are unsuitable for their growth, survival, and reproduction. The vast spatial extent of the tsunami and the subsidence strongly suggest that such negative effects might have occurred at a broad scale, encompassing entire meta-populations. The benthic meta-population size could therefore decrease with subsequent reduction of recruitment at a broad scale. Additionally, modification of coastal topography by the earthquake (Field et al. 1982) could change the passive larval transport processes of larvae, consequently altering the spatial pattern of larval recruitment at local to intermediate scales. Moreover, mortality caused by the tsunami and subsidence could change the main factors affecting the relative importance of recruitment on population dynamics—free space availability (Gaines and Roughgarden 1985) and population structure (Roughgarden et al. 1985)—with the relative contribution of larval recruitment intensity as a determinant of local population growth rate increasing accordingly after the earthquake. Several studies have reported on the influences of large earthquakes and accompanying tsunamis or coseismic uplift on the distribution and abundance of intertidal sessile organisms (Bodin and Klinger 1986, Castilla 1988, Duran and Castilla 1989, Castilla et al. 2010). However, there are no previous reports on how earthquakes change the population dynamics of rocky intertidal sessile organisms. Likewise, no previous quantitative studies examined the influences of coseismic subsidence on rocky intertidal sessile assemblages, except for evaluations of changes in position of zonation of sessile organisms (Haven 1972, Johansen 1972, Noda et al. 2016a, b).

Acorn barnacles should be ideal for testing various hypotheses about the influence of the 2011 earthquake on population dynamics of rocky intertidal sessile organisms because their life histories are well understood (Connell 1961, 1985, Crisp 1976, Roughgarden et al. 1985, Gaines and Bertness 1992, Miyamoto et al. 1999). In addition, it is easy to quantify the distribution and abundance of both the benthic population and recruitment. *Chthamalus challengeri* is the dominant sessile animal in the mid to high intertidal zone along rocky shores of northern Japan (Nakaoka et al. 2006). This species has its highest seasonal recruitment from July to October (Iwaki 1975), and individuals live several years (Miyamoto et al. 1999).

The purpose of this study was to clarify the influence of the 2011 Tohoku Earthquake on the population dynamics of the rocky intertidal barnacle *C. challengeri*, especially focusing on changes in recruitment and on possible causes and consequences of the change. We addressed the following three questions. (1) At local and intermediate scales, how did the spatial patterns of larval recruitment change after the earthquake? (2) At broader spatial scales encompassing the entire meta-population, did larval recruitment intensity change with changes in the stock size after the earthquake? (3) How did the relative importance of larval recruitment as a determinant of local population growth rate change after the earthquake?

Materials and Methods

Census design

A hierarchical nested sampling design (Noda 2004) was used for the layout of study sites, with four or five sites nested within five shores spaced from 2.6 to 7.9 km apart along the Pacific coast of northern Japan (Fig. 1): Myojin, 39°28′N, 142°00′E; Oura, 39°45′N, 141°99′E; Aragami, 39°24′N, 141°58′E; Akahama, 39°21′N, 141°56′E; and Katagishi, 39°20′N, 141°54′E. The shores Myojin and Oura are on Yamada Bay, Aragami is on Funakoshi Bay, and Akahama and Katagishi are on Otsuchi Bay. Detailed descriptions of the study sites and biogeographic features of the area can be found in previous works (Okuda et al. 2004, Nakaoka et al. 2006, Fukaya et al. 2010)

Within each shore, the four or five sites were haphazardly chosen from semi-exposed locations, with distances between neighboring sites ranging from 7.8 to 209 m (mean±SD, 59.2±70.3 m). At each site, adjacent recruitment and control plots separated by several tens of centimeters were marked with permanent anchors drilled into roughly vertical rock. The plots were 100 cm high, and their vertical midpoints corresponded to the mean tidal level. The recruitment and control plots were 50 and 30 cm wide, respectively. The 100-cm-high plots covered 72.4% of the mean spring-tide tidal range of 138.2 cm.

In March 2011, subsidence occurred along the study area due to the earthquake. Therefore, in July 2011, 4 months after the earthquake, we vertically extended control plots (100 cm high and 50 cm wide) with their lower borders sharing the top border of each control plot, so that the vertical observation range was 200 cm. In April 2012, we also rees-

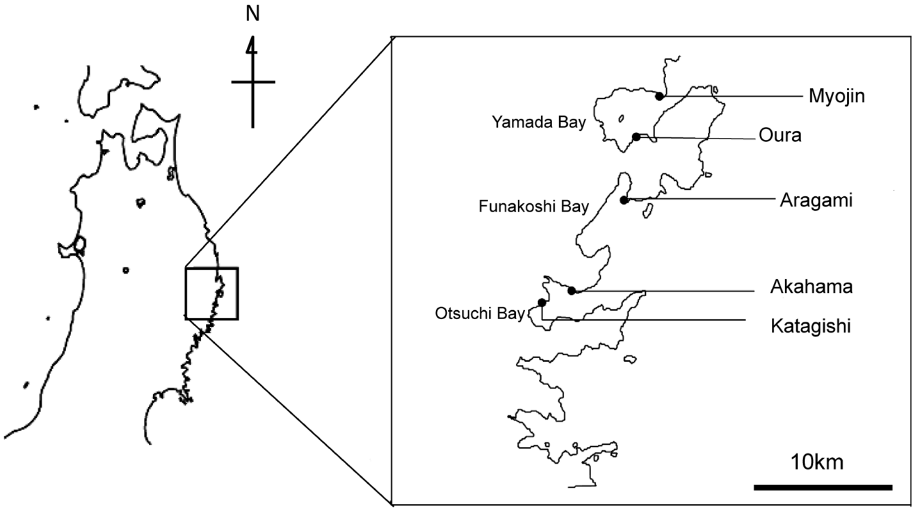

Fig. 1. Map showing study sites. Five rocky shores were chosen for a census of intertidal organisms along the Pacific coast of Japan.

Table 1. The results of nested ANOVA of the logarithm of the ratio of mean annual recruitment density after the 2011 earthquake to annual recruitment density before the earthquake for (a) 2012 and (b) 2013.

(a)

Source	df	MS	*F*	*P*
Shore	4	9.77	2.90	0.05
Site	18	3.37	11.58	<0.001
Year	69	0.29		
Total	91	1.32		

(b)

Source	df	MS	*F*	*P*
Shore	4	1.40	0.41	0.80
Site	18	3.41	11.70	<0.001
Year	69	0.29		
Total	91	0.96		

tablished recruitment plots (100 cm high by 30 cm wide) at the same locations, centered at the mean tidal level.

Recruitment plots were cleared of all surface organisms each April and July during low tide by burning and then scraping the rock surface with a wire brush. Recruitment plots were observed each July and October, first from 2004 to 2007 (before the earthquake) and then in 2012 and 2013 (after the earthquake). Sampling of recruitment plots occurred approximately 90 d after they were cleared to assess the magnitude of recruitment during the major recruitment period for *C. challengeri* every year. Sampling of recruitment plots involved photographing 5 cm×5 cm quadrats using a Canon IXY Digital 320 camera (macro setting and 180 dpi at a distance of 10 cm from the plot surface). Forty replicate quadrat photographs were taken within each plot (four replicates from 10 vertically separated areas) and used to estimate the recruitment density (recruits per 25 cm^2) in each plot in each year. The annual recruitment density of *C. challengeri* was calculated by adding the number of recruits for both recruitment seasons.

Control plots were observed each April and October from 2004 to 2007 (before the earthquake) and then in 2012 and 2013. Estimates of the percent coverage by *C. challengeri* were obtained from the same elevational range of the control plot before the earthquake (mean tidal level±50 cm) by using a grid overlain on the plot with observation points at evenly spaced intervals (5 cm vertically and 5 cm horizontally; 200 grid points total), since the vertical position of mode of abundance in the zonation of *C. challengeri* almost recovered to the position of before the earthquake in 2012 (Noda et al. 2015). The presence or absence of *C. challengeri* at each point on the grid was used to estimate the total coverage of *C. challengeri* for each plot at each census.

By using the coverage and recruitment density data on *C. challengeri*, we obtained estimates of mean coverage and recruitment density at three spatial scales, shore, bay and regional scales. Estimates at the bay scale were obtained from the bays that included sites at two shores: Otsuchi Bay and Yamada Bay (Fig. 1). Values at the regional scale were obtained using data from sites at all five shores. Furthermore, the local population growth rate was obtained by subtracting the logarithm of coverage in April from the logarithm of coverage in October for each year at each site.

Data analysis

Change in spatial pattern of recruitment

To evaluate the effects of the earthquake on recruitment density, we calculated the logarithm of the ratio of mean annual recruitment density after the earthquake (2012, 2013) to that before the earthquake (2004–2007) for each year combination using the following formula:

$$d_{ij}=\log_{10}(Q_i)-\log_{10}(Q_j) \quad (1)$$

where the d_{ij} is the log ratio of annual recruitment density in post-earthquake year i (i=2012 or 2013) to that in pre-earthquake year j (j=2004, 2005, 2006, or 2007), and Q_i and Q_j are the annual recruitment densities in post-earthquake year i and pre-earthquake year j, respectively. A Nested ANOVA was performed to examine whether the d_{ij} values were different among shores or sites.

To assess how the spatial consistency of annual recruitment density among sites changed after the earthquake, we determined Spearman's rank correlation coefficient (r_s) for three types of comparisons of years: (1) among the 4 years before the earthquake (six combinations), (2) between 2012 and each year of sampling before the earthquake (four combinations), and (3) between 2013 and each year of sampling before the earthquake (four combinations).

Change in recruitment arising from alteration of stock size

To evaluate the changes in annual recruitment density and adult population size before and after the earthquake at bay and regional scales, we obtained effect sizes from before the earthquake to after by the following formulas:

$$\text{Effect size of coverage} = \frac{\log_{10}(P_i)-\log_{10}(P_{\text{mean } j})}{P_{\text{sd } j}} \quad (2)$$

$$\text{Effect size of mean recruitment density} = \frac{\log_{10}(Q_i)-\log_{10}(Q_{\text{mean } j})}{Q_{\text{sd } j}} \quad (3)$$

where P_i, and P_j are the coverage averaged at bay or regional scales in April of post-earthquake year i (i=2012 or 2013) and pre-earthquake year j (j=2004, 2005, 2006, or 2007), respectively. $P_{\text{mean}j}$ and $P_{\text{sd}j}$ are their mean and standard deviation of P_j before the earthquake, respectively. Q_i and Q_j are the annual recruitment densities at bay or regional scales in post-earthquake year i and pre-earthquake year j, respectively, and $Q_{\mathrm{mean}j}$ and $Q_{\mathrm{sd}j}$ are their mean and standard deviation of Q before the earthquake, respectively. An absolute value for the effect size greater than 1.96 indicates that the coverage (or recruitment density) in the post-earthquake year (2012 or 2013) deviated significantly from the range of fluctuations among pre-earthquake years with a risk of type I error of 5%. Alternatively, Cohen (1988) suggested that an absolute values of effect sizes from 0.2 to 0.3 might be considered a “small” effects, around 0.5 as “medium” effects, and 0.8 to infinity as “large” effects.

The stock–recruitment relationships were examined at both regional and bay scales because the larval period of barnacles (Iwaki 1992) is similar to the flushing times of the bays (Hirano and Hayakawa1976). At both scales, we examined the association between the interannual variation in recruitment and the stock–recruitment relationship using linear regression of the logarithm of mean annual recruitment density against the logarithm of mean coverage in April over the census period.

At the bay scale, we examined whether the stock–recruitment relationship differed among bays. We first performed multiple regression analysis in which the logarithm of annual recruitment density in each bay in each year was treated as a response variable and the mean coverage in each bay in April (fixed factor), the bay (fixed factor), and an interaction term between these two fixed factors were treated as predictors. The best set of predictors was selected based on Akaike’s information criterion (AIC; Akaike 1974). The best model included a single predictor: the mean coverage in each bay. We therefore examined the association between the interannual variation in recruitment and the stock–recruitment relationship at the bay scale using a linear regression of the logarithm of mean annual recruitment density against the logarithm of mean coverage in April over the census period.

Change in importance of recruitment as a determinant of local population growth rate

To examine how the relative importance of larval recruitment as a determinant of local population growth rate changed after the earthquake, we performed linear regression analysis of the logarithm of local population growth rate against the logarithm of annual recruitment density over three time periods: before the earthquake, 2012, and 2013. The density-dependence of the local population growth rate was tested by checking whether the regression slope significantly deviated from 1.0. On a log–log scale, a slope of 1.0 signifies constant mortality across all densities, or density independence (e.g., Caley et al. 1996, Hixon 1998). Slopes >1.0 and <1.0 indicate positive and negative density-dependent effects, respectively.

Results

Change in spatial pattern of recruitment

Nested ANOVA showed that d_{ij} values for both 2012 and 2013 were significantly different among sites, whereas there were no significant differences among shores (Table 1). In both 2012 and 2013, lower limit of the 95% confidence interval for d_{ij} was greater than zero at 4 sites, whereas the upper limit of the 95% confidence interval for d_{ij} was less than zero at 2 sites (Fig. 2), suggesting that spatial patterns of recruitment slightly changed after the earthquake.

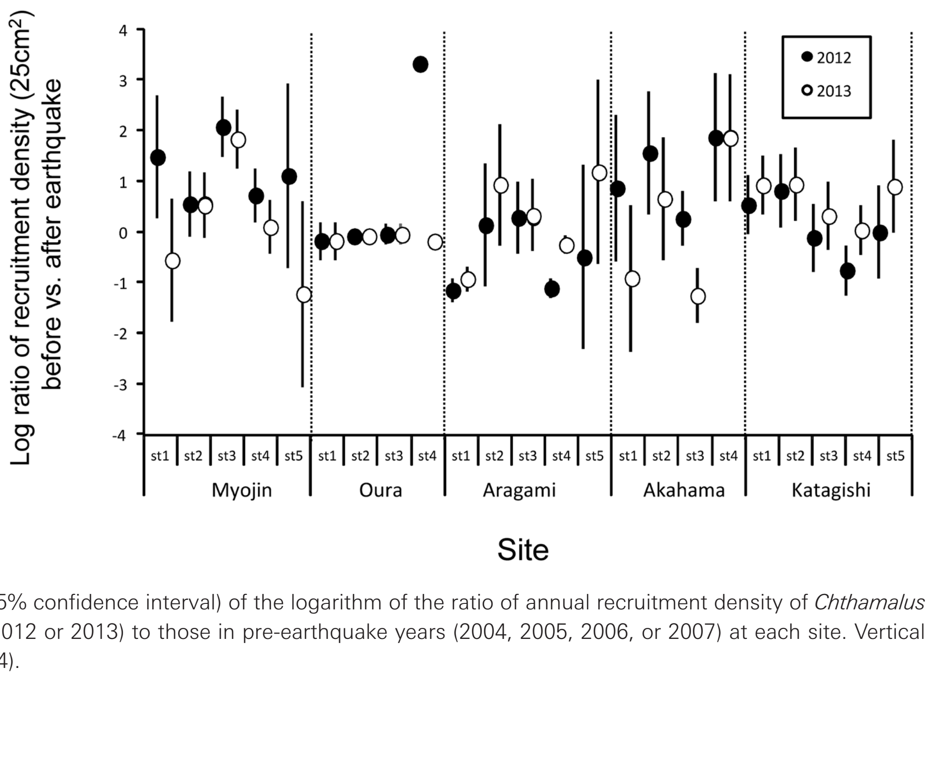

Fig. 2. Mean (±95% confidence interval) of the logarithm of the ratio of annual recruitment density of *Chthamalus challengeri* in post-earthquake years (2012 or 2013) to those in pre-earthquake years (2004, 2005, 2006, or 2007) at each site. Vertical bars indicate standard deviations (n=4).

The spatial consistency of annual recruitment density at each site within the same shore did not change notably after the earthquake. There were no clear differences among the Spearman's rank correlation coefficients (r_s) for three comparisons between years: (1) among the 4 years before the earthquake, (2) between 2012 and each year before the earthquake, and (3) between 2013 and each year before the earthquake (Fig. 3).

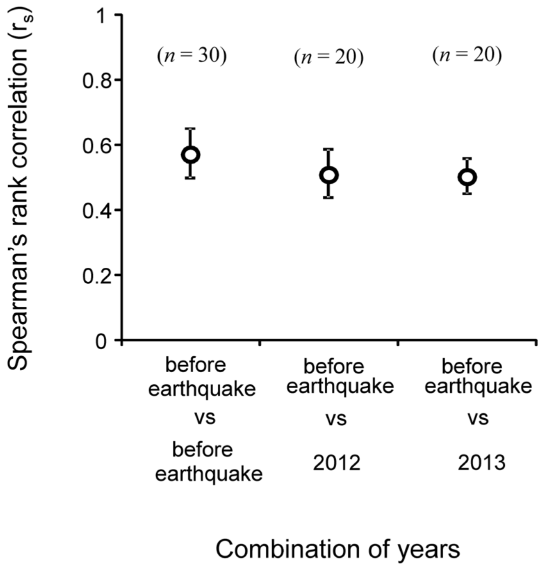

Fig. 3. Mean (±standard error) of Spearman's rank correlation (r_s) between annual recruitment densities at all sites from different years showing how the spatial consistency of annual recruitment density of *Chthamalus challengeri* at each site within the same shore changed after the earthquake. Years used for comparisons: (1) among four sampling years before the earthquake (2004–2007), (2) between 2012 and each year before the earthquake, and (3) between 2013 and each year before the earthquake.

Change in recruitment arising from alteration of stock size

Regional scale

At the regional scale, the annual recruitment density was significantly and positively correlated with the mean coverage in April (Fig. 4a), suggesting that interannual changes in recruitment density arose from an alteration of the stock size at the regional scale. In both 2012 and 2013, the effect sizes of both the coverage and the mean recruitment density were positive (Table 2). In 2012, the effect sizes of both coverage and mean recruitment density were greater than 1.96. In 2013, the effect sizes of both the coverage and the recruitment density were less than in 2012, but the effect size of the coverage was still greater than 1.96. The effect size of the recruitment density for 2013 was less than 1.96 but greater than 0.8, suggesting that the effect of the earthquake on recruitment was "large," as defined by Cohen (1988).

Table 2. The effect size of recruitment density and coverage before the earthquake to each year after earthquake (2012, 2013) in Yamada Bay (YM), Otsuchi Bay (OT), and for all bays (Regional).

		Effect size	
		Coverage	Recruitment density
Bay scale			
2012	YM	4.66	2.78
	OT	6.13	2.28
2013	YM	3.40	1.49
	OT	1.33	2.21
Regional scale			
2012		6.53	2.14
2013		3.01	1.47

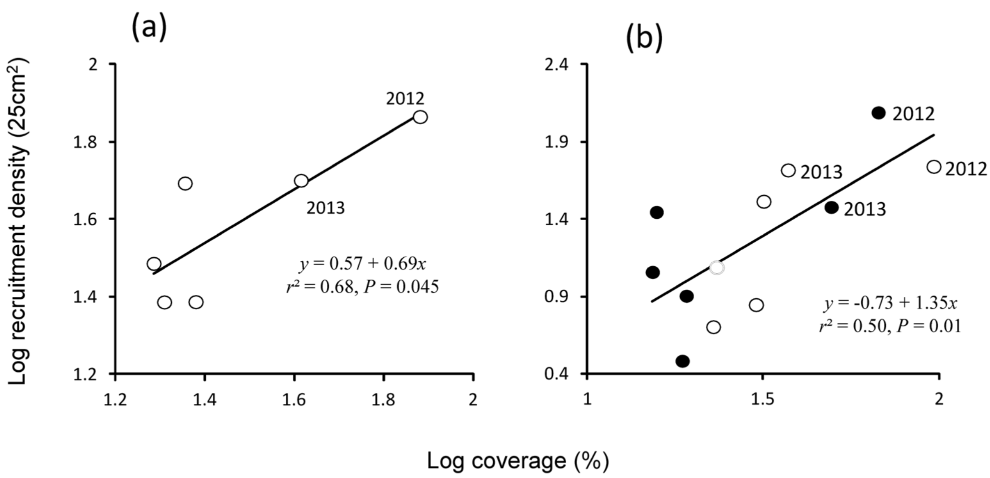

Fig. 4. Regression of annual recruitment density against mean coverage of *Chthamalus challengeri* on (a) the regional scale, and (b) the bay scale (open and solid circles are Otsuchi Bay and Yamada Bay, respectively). Estimated regression equations and fitted lines are shown.

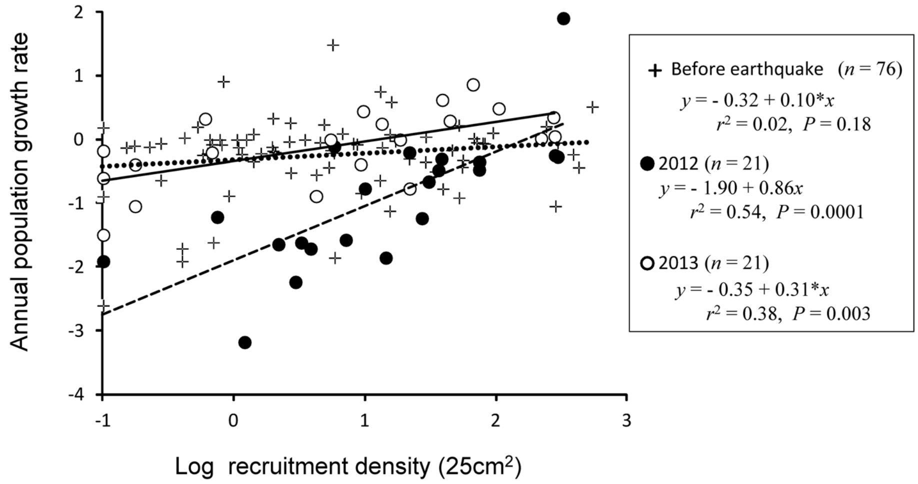

Fig. 5. Regression of the population growth rate in each plot against the annual recruitment density of *Chthamalus challengeri*. Estimated regression equations and fitted lines are shown. The dotted, dashed, and solid lines represent the years before the earthquake (2004–2007), 2012, and 2013, respectively. The asterisks next to the regression coefficients indicate that the values differ from 1 at a significance level of $P<0.05$.

Bay scale

At the bay scale, the annual recruitment density was significantly and positively correlated with the mean coverage in April (Fig. 4b), suggesting that interannual changes in recruitment intensity arose from an alteration of stock size at the bay scale. In both 2012 and 2013, the effect sizes of both the coverage and the mean recruitment density were positive (Table 2). In 2012, the effect sizes of both the coverage and the mean recruitment density were greater than 1.96. In 2013, the effect sizes of both the coverage and the recruitment density were less than in 2012 for each bay, although the effect sizes of both the coverage in Yamada Bay and the recruitment density in Otsuchi Bay were greater than 1.96. The effect sizes of both the recruitment density in Yamada Bay and the coverage in Otsuchi Bay in 2013 were less than 1.96 but greater than 0.8, suggesting that these effects of the earthquake were “large,” as defined by Cohen (1988).

Change in the importance of recruitment as a determinant of local population growth rate

Linear regression analysis suggested that the importance of larval recruitment as a determinant of the local population growth rate changed after the earthquake (Fig. 5). Before the earthquake, the regression of local population growth rate against annual recruitment density was not significant, suggesting that the local population growth rate was independent of recruitment density and that there was density-dependent mortality. In contrast, in 2012 the local population growth rate was significantly and positively correlated with the annual recruitment density, and the slope of the regression was not significantly different from 1.0, suggesting that the local population growth rate depended on recruitment density and this dependence was density independent. In 2013, the local population growth rate was significantly and positively correlated with the annual recruitment density, and the slope of the regression was significantly less than 1.0, suggesting that the local population growth rate depended on both recruitment density and other density-dependent factors.

Discussion

Changes in spatial pattern of recruitment

The results of both the nested ANOVA examining the spatial variability of $\underline{d_{ij}}$ and the comparison of $\underline{r_s}$, which assessed the spatial consistency of recruitment patterns, demonstrated that the spatial pattern of larval recruitment after the earthquake did not differ from that before the earthquake (Figs. 2, 3). This result suggests that the passive transport process, which is a major determinant of larval supply, did not change after the earthquake, or that the passive transport process changed after the earthquake while maintaining its spatial consistency among sites. Within and around the study sites, there were no signs of coastal cliff failure or landslides associated with the earthquake (T. Noda, pers. obs.), which might have altered the passive larval transport process via modification of coastal topography. The subsidence from the earthquake could have resulted in increased wave speed, and consequently increased larval flux, while maintaining spatial consistency. This is because the range of subsidence was consistently about 50 cm throughout the observation area (Iida 2013, Noda et al. 2016a) and wave speed at depths shallower than several meters is proportional to the square root of water depth (Denny and Wethey 2001).

Change in recruitment arising from alteration of stock size

It is plausible that the 2011 earthquake off the Pacific coast of Tohoku, which generated a large tsunami and resulted in subsidence of 35–70 cm over the entire Tohoku region (Okada 2011), severely damaged the population of rocky intertidal barnacles in this region. Kendall et al. (2009) demonstrated that a tsunami eroded and redeposited sediment and transported floating wreckage, in the process smothering or scouring rock surfaces and consequently causing the mass mortality of barnacles. In addition, the subsidence of 35–70 cm resulting from the 2011 earthquake could have shifted barnacles to near the lower limit of their vertical range, where they often suffer from high mortality from predation or competition (Luckens 1975). Additionally, the vast spatial extent of the tsunami and subsidence obviously encompassed an entire meta-population of barnacles, thereby presumably reducing the recruitment of larvae as a consequence of a large decline in the stock size at a broad scale, as Peterson and Summerson (1992) found for the bay scallop, where recruitment at a broad scale was drastically reduced and proportional to the adult population after a red tide severely decimated the adults.

In contrast to these predictions, however, the present study showed that the population size of *C. challengeri* increased over a large geographic scale just after the March 2011 earthquake, with a consequent increase in recruitment intensity. This is because the annual recruitment density was significantly and positively correlated with the mean coverage in April, and the effect size values of both the coverage and the mean recruitment density were greater than 1.96 in 2011, suggesting that population size and recruitment density significantly increased after the earthquake (Fig. 4, Table 2).

Noda et al. (2015) demonstrates that *C. challengeri* shifted its zonation downward according to the subsidence in 2011, then expanded its zonation it upward in 2012. This finding indicates that the increase of *C. challengeri* right after the earthquake result from two causes which are not mutually exclusive. First, it is possible that *C. challengeri* did not suffer mass mortality from the tsunami and subsidence (Iwasaki et al. 2016). Indeed, coverage of *C. challengeri* in control plots in July 2011, immediately after the earthquake, was not significantly different from that in October 2010, right before the earthquake (Noda, T. unpublished data). Second, there might have been a high level of larval recruitment of *C. challengeri* to its normal vertical range within the first year after earthquake. Indeed, although the coverage in post-earthquake control plots was extremely low just after the earthquake (July 2011), it reached at an exceptionally high level in July 2012 (Fig. S1a), before the main recruitment season for *C. challengeri* (i.e., July to October; Iwaki 1975).

Change in the importance of recruitment as a determinant of local population growth rate

The linear regression analyses of population growth rate against recruitment showed that the dependence of local population growth rate on larval recruitment increased after the earthquake (Fig. 5). This might be explained by the fact that free space was notably abundant in July 2012 and April 2013 compared to before the earthquake (Noda, T. unpublished data). It is known that the importance of recruitment to population dynamics increases with an increase in the availability of free space (Todd 1998).

Conclusions

The present study demonstrated that whereas the spatial pattern of larval recruitment of *C. challengeri* was only slightly affected by the 2011 earthquake off the Pacific coast of Tohoku, the population dynamics were significantly different immediately (1–2 years) after the earthquake at two spatial scales. At a broad spatial scale encompassing several bays, its population size increased, consequently enhancing recruitment intensity, whereas at a local scale, the dependence of local population growth rate on larval recruitment increased. The most interesting finding is that the population of this barnacle significantly increased just after the events accompanying the earthquake at a broad spatial scale, whereas it has been widely assumed that severe physical disturbances at a broad spatial scale heavily affect natural populations in general. Indeed, previous large earthquakes have resulted in the mass mortality of various rocky intertidal organisms (Castilla 1988, Castilla et al. 2010). Such a contradiction between previous reports and our findings could be related to differences in the direction of coseismic vertical movements: all previous studies involved cases of coseismic uplift. Future studies to test this hypothesis are eagerly anticipated, as it appears that our study is the first to report the impact of coseismic subsidence on population dynamics of rocky sessile organisms. Another promising future research direction would be to clarify the ecological consequences of the increase in *C. challengeri* in the rocky intertidal communities in this region. This is because this barnacle is a dominant species among the sessile assemblages (Fukaya et al. 2010), being consumed by various invertebrates such as whelks and sea stars (Hori and Noda 2001), and competing for space with other sessile organisms such as other barnacles, mussels, and seaweeds (Miyamoto et al. 1999, Chiba and Noda 2000, Kado 2003).

Acknowledgments

We are grateful to T. Okuda, M. Tsujino, T. Hagino, M. Iida, R. Sahara, M. Ohira, and Y. Kanamori for field assistance. For field and laboratory facilities, we are grateful to the staff and students of the International Coastal Research Center of the Atmosphere and Ocean Research Institute, University of Tokyo. This study was made possible by the generous support and encouragement of local fisherman and the fishery office of the Fisherman's Cooperative Associations in Iwate. This research was supported by the Cooperative Program of the Atmosphere and Ocean Research Institute, University of Tokyo (nos. 108, 104, 107, 101, and 103 in 2006, 2007, 2008, 2009, and 2010, respectively, to T.N.), and was partly supported by JSPS KAKENHI Grant (Nos. 20570012, 24570012 and 15K07208 to TN) and the Tohoku Ecosystem-Associated Marine Sciences (TEAMS) project. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

References

Akaike, H. 1974. A new look at the statistical model identification. IEEE Trans Automat Control 19: 716–723.

Bodin, P. and Klinger, T. 1986. Coastal uplift and mortality of intertidal organisms caused by the September 1985 Mexico Earthquakes. Science 233: 1071–1073.

Caley, M. J., Carr, M. H., Hixon, M. A., Hughes, T. P., Jones, G. P. and Menge, B. A. 1996. Recruitment and the local dynamics of open marine populations. Annu Rev Ecol Syst 27: 477–500.

Castilla, J. C. 1988. Earthquake-caused coastal uplift and its effects on rocky intertidal kelp communities. Science 242: 440–443.

Castilla, J. C., Manríquez, P. H. and Camaño, A. 2010. Effects of rocky shore coseismic uplift and the 2010 Chilean mega-earthquake on intertidal biomarker species. Mar Ecol Prog Ser 418: 17–23.

Chiba, S. and Noda, T. 2000. Factors maintaining topography-related mosaic of barnacle and mussel on a rocky shore. J Mar Biol Assoc UK 80: 617–622.

Cohen, J. 1988. Statistical power analysis for the behavioral sciences (2nd ed.). Lawrence Earlbaum Associates, Hillsdale

Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecolog*y 42**:** 710–723.

Connell, J. H. 1985. The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. J Exp Mar Biol Ecol 93*:*11–45.

Crisp, D. J. 1976. Settlement responses in marine organisms. *In* Adaptation to environment: essays on the physiology of marine animals. Newell, R.C. (ed.), pp. 83–124, Butterworths, London

Denny, M. and Wethey, D. 2001. Physical processes that generate patterns in marine communities. *In* Marine community ecology. Bertness, M.D., Gaines, S.D. and Hay, M.E. (eds.), pp. 3–37, Sinauer Associates Inc, Sunderland

Duran, L. R. and Castilla, J. C. 1989. Variation and persistence of the middle rocky intertidal community of central Chile, with and without human harvesting. Mar Biol 103: 555–562.

Field, M. E., Gardner, J. V., Jennings, A. E., and Edwards, B. D. 1982. Earthquake induced sediment failures on a 0.25 ° slope, Klamath River delta, California. Geology 10: 542–546.

Fukaya, K., Okuda, T., Nakaoka, M., Hori, M. and Noda, T. 2010. Seasonality in the strength and spatial scale of processes determining intertidal barnacle population growth. J Anim Ecol 79: 1270–1279.

Gaines, S. D. *and* Bertness, M. D. 1992. Dispersal of juveniles and variable recruitment in sessile marine species. Nature 360*:* 579–580.

Gaines, S. D. and Roughgarden, J. 1985. Larval settlement rate: a leading determinant of structure in an ecological community of the marine intertidal zone. Proc Natl Acad Sci USA 82: 3707–3711.

Haven, S. B. 1972. Effects of land level changes on intertidal invertebrates with discussion of postearthquake ecological succession. *In* The great Alaska earthquake of 1964: Biology. National Academy of Science, Publication 1604. Committee on the Alaska Earthquake of the Division of Earth Sciences National Research Council (ed.), pp. 82–106. National Academy of Science, Washington DC

Hirano, T. and Hayakawa, T. 1976. Water mass and diffusion of river water in Otsuchi Bay. Otsuchi Mar Res Center Rep 2: 49–59.

Hixon, M.A. 1998. Population dynamics of coral-reef fishes: controversial concepts and hypotheses. Austral J Ecol 23: 192–201.

Hori, M. and Noda, T. 2001. Spatio-temporal variation of avian foraging in the rocky intertidal food web. J Anim Ecol 70: 122–137.

Hughes, T. P., Baird, A. H., Dinsdale, E. A., Moltschaniwskyj, N. A., Pratchett, M. S., Tanner, J. E. and Willis, B. L. 2000. Supply-side ecology works both ways: the link between benthic adults, fecundity and larval recruits. Ecology 81: 2241–2249.

Iida, M. 2013. Impact of the 2011 Tohoku Earthquake on rocky intertidal community. Unpublished master's degree dissertation, Hokkaido University.

Iwaki, T. 1975. Breeding and settlement of *Chthamalus challengeri* Hoek on the southern coast of Hokkaido. Bull Fac Fish Hokkaido Univ 26: 1–10.

Iwaki, T. 1992. On the seasonal conformity among breeding, larval occurrence and settlement of barnacles. Bull Fac Bioresources Mie Univ 7:37–46.

Iwasaki, A., Fukaya, K. and Noda, T. (2016) Quantitative evaluation of the impact of the Great East Japan Earthquake and tsunami on the rocky intertidal community. *In* Ecological impacts of tsunamis on coastal ecosystems: lessons from the Great East Japan Earthquake, Ecological research monographs. Urabe, J. and Nakashizuka, T. (eds.), pp. 35–46, Springer, Tokyo

Johansen, H. W. 1972. Effects of elevation changes on benthic algae in Prince William Sound. *In* The great Alaska earthquake of 1964: Biology. National Academy of Science, Publication 1604. Committee on the Alaska Earthquake of the Division of Earth Sciences National Research Council (ed.), pp. 35–68. National Academy of Science, Washington DC

Kado, R. 2003. Invasion of Japanese shores by the NE Pacific barnacle *Balanus glandula* and its ecological and biogeographical impact. Mar Ecol Prog Ser 249: 199–206.

Kendall, M. A., Aryuthaka, C., Chimonides, J., Daungnamon, D., Hills, J., Jittanoon, C., Komwachirapitak, P., Kongkaew, V., Mittermeyr, A., Monthum, Y., Nimsantijaroen, S., Paterson, G. I. J., Foster-Smith, R., Foster-Smith, J. and Thongsin, N. 2009. Post-tsunami recovery of shallow water biota and habitats on Thailand's Andaman coast. Polish J Environ Stud 18: 69–75.

Luckens, P. A. 1975. Predation and intertidal zonation of barnacles at Leigh, New Zealand. New Zeal J Mar Fresh 9: 355–378.

Miyamoto, Y., Noda, T. and Nakao, S. 1999. Zonation of two barnacle species not determined by competition. J Mar Biol Assoc UK 79: 621–628.

Nakaoka, M., Ito, N., Yamamoto, T., Okuda, T. and Noda, T. 2006. Similarity of rocky intertidal assemblages along the Pacific coast of Japan: effects of spatial scales and geographic distance. Ecol Res 21: 425–435.

Noda, T. 2004. Spatial hierarchical approach in community ecology: a way beyond high context-dependency and low predictability in local phenomena. Popul Ecol 46: 105–117.

Noda, T. Iwasaki, A. and Fukaya, K. (2016a) Recovery of rocky intertidal zonation: two years after the 2011 Great East Japan Earthquake. J Mar Biol Assoc UK 96: 1549–1555.

Noda, T. Iwasaki, A. and Fukaya, K. (2016b) Rocky intertidal zonation: impacts and recovery from the Great East Japan Earthquake. *In* Ecological impacts of tsunamis on coastal ecosystems: lessons from the Great East Japan Earthquake, Ecological research monographs. Urabe, J. and Nakashizuka, T. (eds.), pp. 25–34, Springer, Tokyo

Okada, Y. 2011. Preliminary report of the 2011 Tohoku Earthquake. http://www.bosai.go.jp/e/pdf/Preliminary_report110328.pdf (last accessed March 27, 2015)

Okuda, T., Noda, T., Yamamoto, T., Ito, N. and Nakaoka, M. 2004. Latitudinal gradient of species diversity: multi-scale variability in rocky intertidal sessile assemblages along the North Western Pacific coast. Popul Ecol 46: 159–170.

Peterson, C. H. and Summerson H. C. 1992. Basin-scale coherence of population dynamics of an exploited marine invertebrate, the bay scallop: implications of recruitment limitation. Mar Ecol Prog Ser 90: 257–272.

Roughgarden, J., Iwasa, Y. and Baxter, C. 1985. Demographic theory for an open population with space-limited recruitment. Ecology 66: 54–67.

Shanks, A. L. 1995. Mechanisms of cross-shelf dispersal of larval invertebrates and fish. *In* Ecology of marine invertebrate larvae. McEdward, L. (ed.), pp. 323–368, CRC Press, Boca Raton

Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. Biol Rev Camb Philos Soc 25: 1–45.

Todd, C. D. 1998. Larval supply and recruitment of benthic invertebrates: do larvae always disperse as much as we believe? Hydrobiologia 375/376: 1–21.