HOKKAIDO UNIVERSITY

Title	Quantifying intensity and severity of natural disturbances : a case study of the impact of the 2011 Tohoku Earthquake Tsunami on rocky intertidal community
Author(s)	岩﨑, 藍子
Degree Grantor	北海道大学
Degree Name	博士(環境科学)
Dissertation Number	甲第13112号
Issue Date	2018-03-22
DOI	https://doi.org/10.14943/doctoral.k13112
Doc URL	https://hdl.handle.net/2115/70366
Type	doctoral thesis
File Information	Aiko_Iwasaki.pdf

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Quantifying intensity and severity of natural disturbances: a case study of the impact of the 2011 Tohoku Earthquake Tsunami on rocky intertidal community

Thesis

In partial fulfillment of the requirements for

The degree of Doctor of Environmental Science

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March, 2018, Sapporo

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Summary

Chapter I

1. Prediction of the impact of natural disturbances on an ecosystem is an important task of ecologists. The impact of disturbance at various ecological levels (e.g., population, community and ecosystem) may depend primarily on the intensity, which is defined as the physical strength of the disturbing force (e.g., wind speed (m/s) for a hurricane), disturbance type (e.g., drought, wildfire, and hurricane), and species vulnerability. However, it remains largely unknown how the severity of disturbance impact was determined integratively by those factors.
2. General understanding of the disturbance impact is greatly contributed by quantitative comparison of the severity of disturbance impact across types of event and species. Previous comparative researches about the severity of disturbance impacts can be classified into several types. In all types of comparative studies, there are small number of synthetic study that quantitatively compare the severity of disturbance impacts, especially for studies comparing the severity of disturbance impacts on many species across various disturbance types.
3. There are two serious methodological drawbacks in all of previous studies which quantitatively compared severity of disturbance impacts. First, severity of single disturbance event among different species was evaluated based on changes in population size before and after the event without taking any account of species-specific natural variability in abundance. Second, no study quantitatively compared the disturbance impact across various disturbance types based on the disturbance intensity due to differences in the physical units of the force strength among disturbance events. Thus, these two drawbacks should be overcome to establish a framework for quantitative comparison of the severity of disturbance impacts across species and disturbance types,

Chapter II

1. It has been widely assumed that tsunamis associated with mega-earthquakes severely damage coastal ecosystems. In no previous studies, however, have the community-level impacts of tsunamis been credibly quantified.
2. I rigorously evaluated the impacts of the tsunami following the Tohoku Earthquake on species abundances in a rocky intertidal metacommunity encompassing 30 km of shoreline located 150–160 km north-northwest of the epicenter of the earthquake.
3. For this purpose, we generated an indicator of the tsunami impact—the change in mean abundances between before and after the tsunami, standardized to population variability before the earthquake—for each of five sessile and six mobile species. We then used the averaged values of this indicator as a quantitative measure of tsunami impacts for the entire community and for the sessile and mobile subgroups.
4. The tsunami had an overall significant negative impact on the rocky intertidal community at the regional scale, although the negative impact seemed smaller than those of similar large-scale disturbances on rocky intertidal communities. There was a significant negative impact of the tsunami on mobile species, but not on sessile species. This suggests that mobile species on rocky shores are more vulnerable than sessile species to tsunamis. I conclude that the rocky intertidal community had a significant impact but minor damage from the tsunami caused by the Tohoku Earthquake at the regional scale.

Chapter III

1. Understanding the impacts of natural disturbances on wildlife populations is a central task for ecologists; in general, the severity of impact of a disturbance (e.g., the resulting degree of population decline) is likely to depend primarily on the disturbance intensity (i.e., strength of forcing), type of disturbance, and species vulnerability. However, differences among disturbance events in the physical units of forcing and interspecific differences in the temporal variability of population size under normal (non-disturbance) conditions hinder comprehensive analysis of

disturbance severity.

2. Here, we propose new measures of disturbance intensity and severity, both represented by the return periods. We use a meta-analysis to describe the severity–intensity relationship across various disturbance types and species.
3. The severity and the range of its 95% confidential interval increased exponentially with increasing intensity. This nonlinear relationship suggests that physically intense events may have a catastrophic impact, but their severity cannot be extrapolated from the severity–intensity relationship for weak, frequent disturbance events.
4. The framework I propose may help to clarify the influence of event types and species traits on the severity–intensity relationship, as well as to improve our ability to predict the ecological consequences of various disturbance events of unexperienced intensity.

Chapter IV

1. The interspecific difference in vulnerability to disturbance should depend on species traits which fall into two categories: phenotypic traits (i.e., body size, morphological and physiological properties) and life history traits (i.e., generation time, dispersal ability, and fecundity). Phenotypic traits which play an important role in determining species vulnerability should be largely dependent upon kind of disturbance events, species phylogeny, and habitat types. On the other hands, the role of each life history traits should be relatively consistent across kinds of disturbance.
2. Life history traits affect not only the species vulnerability to disturbance but also the speed of population recovery after disturbance. Thus, our understanding on ecological consequence of disturbances will be greatly contributed by evaluating how the intensity–severity relationship is influenced by event types and species life history traits, but this is a future challenge which can be attained by the framework I proposed in Chapter 3.
3. The framework I propose has broad applicability. First, it can be applied at various spatial or temporal scales and for species with various generation times. Second, it can be used to assess the impacts of disturbances on properties at the community level (e.g., species diversity) and ecosystem level (e.g., productivity), as well as at

the population level (e.g., population growth rate in this study). Third, although it is difficult to quantify the intensity of some anthropogenic disturbances, such as land-use change, pollution, and fishing and harvesting, the framework can be used to assess the interactive effect of anthropogenic disturbances and natural disturbances by comparing the severities of natural disturbances between habitats that are affected and not affected by anthropogenic disturbances. Fourth, by considering severities of anthropogenic disturbances in the severity–intensity relationship obtained from natural disturbances, we can calculate the intensities of such anthropogenic disturbances by assuming that the severities are comparable to those caused by natural disturbances.

4. The framework I propose would allow us to predict the ecological consequences of various kinds of disturbance events at multiple ecological levels (e.g., population, community, and ecosystem). Unfortunately, however, the current lack of long term census data makes these analyses, of especially community and ecosystem-levels, impossible, highlighting the urgent need to conduct long-term censuses of various kinds of organisms in different habitats.

Acknowledgements

I am grateful to Dr. T. Noda, my supervisor, for much guidance, advice, discussion and encouragement in my study. I also thank Dr. T. Takada, Dr. M. Nakaoka and Dr. I. Koizumi for reviewing this thesis. I must show my appreciation to Dr. K. Fukaya for their valuable comments and collaboration. I appreciate Dr. Y. Nishimura for valuable comment for tsunamis. I appreciate Mr. J. L. Anders for providing valuable comment on my manuscript and checking my written English. For field and laboratory facilities, I am grateful to the staff and students of the Akkeshi and Usujiri Marine Station of Hokkaido University, the International Coastal Research Center of the Ocean Research Institute, and the International Coastal Research Center of the Atmosphere and Ocean Research Institute, The University of Tokyo. This study was made possible by the generous support and encouragement of local fishermen and fishery offices of the Federation of fisheries cooperative associations in Hokkaido and Iwate Prefecture. I thank Dr. T. Yamamoto, Dr. M. Hori, Dr. T. Okuda, Dr. M. Tsujino, T. Hagino, Dr. A. Aizawa, Dr. A. K. M. R. Alam, M. Iida, R. Sahara, M. Sakaguchi, Y. Kanamori, M. Ohira, Y. Hiraka, Z. Hu, M. Tachibana, S. Oda, R. Fujii, Y. Noguchi, K. Iwabuchi, K. Ishida, H. Shimizu, T. Abe, Dr. K. Takai, and numerous others for their help with our fieldwork and data analysis, and Dr. K. Kogame and Dr. H. Kajihara for taxonomic identification of algae and marine invertebrates, respectively. I thank R. Iwasaki and many other members of Laboratory of Animal Ecology, Division of Biosphere Science, Hokkaido University for help on my study and their valuable comments. I must be grateful to my sisters' family, Natsumi Itoh, Sei-ichiro Itoh, Aoi Itoh, and Satoki Itoh, my grandparents, Masao Iwasaki, Sayo Iwasaki, Goro Katano and Kikuno Katano, and my parents, Koij Iwasaki and Suzuyo Iwasaki for their supports to my research activities.

Chapter I

General introduction

1.1. Quantitative comparison of disturbance impacts

Prediction of the impact from natural disturbances, such as hurricanes, droughts, and earthquakes on ecosystems is an important task of ecologists (Sousa 1984; Overpeck *et al.* 1990; Gardner *et al.* 2005; Pickett & White 1985; Turner 2010). The severity of impacts on populations, communities and ecosystems (e.g., decline of population size, decrease of diversity, and decrease of productivity) may depend primarily on the disturbance intensity, which is defined as the physical strength of the disturbing force, such as moment magnitude (Mw) for an earthquake or wind speed (m/s) for a hurricane (Pickett & White 1985; Walker 2012). In addition, it is affected by species vulnerability and disturbance type, e.g., drought, wildfire, and hurricane, (Pickett & White 1985; Sousa 2001). However, it remains largely unknown how the severity of disturbance impact was determined integratively by these predictors (Peters *et al.* 2011)

There are two reasons that general understanding of the disturbance impact is greatly improved by quantitative comparison of the severity of disturbance impact across types of events and on individual species. First, it enables us to estimate how the severity−intensity relationship varies across different disturbance types or species. Second, it enables us to estimate the general pattern of severity of disturbance impact with increasing intensity across the disturbance type and species (White & Jentsch 2001; Peters *et al.* 2011).

Previous comparative research about the severity of disturbance impacts can be classified into five categories: 1) comparison of the severity of disturbance impacts on a single species or system across multiple events for a paticular disturbance type, 2)

comparison of severity of disturbance impacts on multiple species within a disturbance event, 3) comparison of severity of disturbance impacts on multiple species or systems across multiple disturbance events for the same disturbance type, 4) comparison of disturbance impacts on a single species or system across disturbance types, and 5) comparison of severity of disturbance impacts on many species or systems across various disturbance types (Table 1-1). In all of the categories of comparative studies on disturbance, there are a surprisingly small number of comprehensive studies that quantitatively compare the severity of disturbance impacts (Peters *et al.* 2011), especially for studies comparing the impacts on many species across various disturbance types.

There are two serious methodological drawbacks in all of the previous studies which quantitatively compared severity of disturbance impacts. First, severity of a single disturbance event among different species was evaluated based on changes in population size before and after a particular disturbance event. This is because observed population changes might not be caused by the disturbance effect alone, but also by species-specific natural variability in abundance. Second, no study quantitatively compared the disturbance impact across various disturbance types based on the disturbance intensity. This is because differences in the physical units of the force strength among disturbance events (e.g., wind speed for hurricanes and moment magnitude for earthquakes) make it impossible to compare the intensity among different disturbance types. Thus, these two drawbacks should be overcome to establish a framework for quantitative comparison of the severity of disturbance impacts across species and disturbance types.

1.2. New framework for quantifying intensity and severity of disturbance events

This thesis aims to provide the framework for comparing the severities of the impact of disturbance across types of events and species, and evaluating the influence of potential predictors, such as intensity and type of disturbance on various species. First, this study focuses on population level severity of the natural and acute disturbances, which cause the mortality immediately after the occurrence. Second, I defined statistical deviation of climatic parameters from normal (non-disturbance) conditions or a certain or more intense destructive event as disturbance events. Third, I estimated the abnormality for

each record of climatic parameters or destructive events as disturbance intensity. Forth, I evaluated the population level severity of disturbance impact based on the normal variability of population growth rate as the reference condition, and estimated the severity as the effect size of mean difference of population growth rate between normal conditions and the year a disturbance event occurred. Finally, I comprehensively evaluated the relationship between the intensity of various types of disturbance events and the severity of impacts on various species.

In the following chapters, I demonstrate quantitative evaluation of the severity of the 2011 Tohoku earthquake and subsequent tsunami on rocky intertidal communities as a case study. I quantify the inter-specific difference in its severity of the event, and placed the severities in the severity–intensity relationship of various disturbance events by performing a meta-analysis. In chapter 2, I evaluated the impacts of the 2011 Tohoku earthquake and tsunami for the entire rocky intertidal community, as well as for the sessile and mobile subgroups. In chapter 3, I propose a framework for quantifying the severity–intensity relationship across various disturbance types and species, and demonstrate the relationship by using a meta-analysis. In chapter 4, I synthesize the results of the previous chapters, and provide future prospects for research in disturbance ecology.

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Table1-1. Comparative researches about the severity of disturbance impacts: category, habitat or organisms, disturbance type, measurement of disturbance impact, explanatory variable(s), and reference.

	Category	Disturbance type	Habitat or organisms	Measurement of disturbance impact	Explanatory variable(s)	Reference
1)	Comparison of severity of disturbance impacts on single species or system across many events within a same disturbance type	Hurricane	Coral reef	Year-to-year rate of change in abundance	-Reef depth (m) -Percent cover of coral before hurricane -Year of study midpoint -Minimum distance from hurricane (km) -Maximum intensity of hurricane (knots) -Average intensity of hurricanes since 1851 (knots) -Time since last hurricane (years) -Average return time between hurricanes (years)	Gardner *et al.* 2005
		Fire	Woodland	-Top kill rate (p) -Root stock mortality (p)	Thermal anormaly (℃・s)	Ryan & Williams 2011
		Hurricane	Coral reef	Bottom cover	Years	Dollar & Tribble 1993
2)	Comparison of severity of disturbance impacts on many species or systems within a disturbance event	Hurricane	-Tropical forest -Temperate Forest	5 classes corresponding to the percentage of wind-thrown trees	-Elevation (m) -Forest type -Aspect -Wind velocity (knot)	Boose *et al.* 1994

Table1-1. Continued

	Category	Disturbance type	Habitat or organisms	Measurement of disturbance impact	Explanatory variable(s)	Reference
		Tsunami	Macrozoobenthic Assemblages in a Shallow Eutrophic lagoon	-Density -Species richness	Before vs After	Kanaya *et al.* 2015
3)	Comparison of severity of disturbance impacts on many species or systems across many disturbance events within same disturbance type	Hurricane	Three species of coral	Mortality rate (% yr^{-1})	Hurricane Hugo/ Intermission/ (Hurricane Marylin/Luis)	Bythell *et al*. 2000
		Fire	Shrub	Change rate in abundance	−	Zedler *et al*. 1983
4)	Comparison of disturbance impacts on single species or system across disturbance types	-Fertilization -Physical disturbance	Grass community	Community dispersion	-Fertilizer(m/g) -Biomass removed (+/-)	Houseman *et al*. 2008
		-Grazing, -Fire	Tall grass prairie	-Cover -Diversity index(H)	-Grazing (+/-) -Burned (+/-)	Collins 1987
		-Fire -Forest fragmentation -Logging	Understory birds	Dissimilarity of community composition	−	Barlow *et al*. 2006

Table1-1. Continued

	Category	Disturbance type	Habitat or organisms	Measurement of disturbance impact	Explanatory variable(s)	Reference
		-Tillage -Grazing -Fire -Agriculture -Logging -Pestcide -Habitat loss	Bee	-Mean difference effect size of abundance -Mean difference effect size of species richness	Habitat loss (++/+)	Winfree *et al*. 2009
		-Hurricane -Drought	River shrimp	Total abundance (no./pool)	Event	Covich *et al*. 2006
5)	Comparison of severity of disturbance impacts on many species or systems across various disturbance types	-Weather -Human perturbation -Thermal stress -Desiccation -Starvation -Oxygen stress -Toxicity -Multiple stressor -Biotoxicity -Disease	-Birds -Fishes -Marine invertebrates -Mammals -Reptiles -Amphibians	Number of death	Year	Fey *et al*. 2015

Chapter II

Quantitative Evaluation of the Impact of the 2011 Tohoku earthquake tsunami on the Rocky Intertidal Community

2.1. Introduction

It has been widely assumed that tsunamis associated with mega-earthquakes severely damaged coastal ecosystems (Lomovaski *et al.* 2011; Rife 2014) because of the tremendous strength of the wave forces and their vast spatial coverage, encompassing entire metapopulations of most coastal organisms. Indeed, many previous reports have documented that tsunamis cause mass mortality of coastal marine populations (e.g. Lomovasky *et al.* 2011; Jaramillo *et al.* 2012; Seike *et al.* 2013). Most of previous studies that reported the community-level effect of tsunamis are not necessarily sufficient for evaluating the direct impacts of tsunami's disturbance on coastal communities for several reasons. First, most of these studies estimated the damage by using only one or a few species (Campbell *et al*. 2007; Takami *et al*. 2013). In such cases the stochastic effect of selecting a species for sampling, which strengthens the influence of an individual species' properties on the estimated susceptibility to tsunamis, can become too large to obtain a general picture of community-level impacts of the tsunami. Second, most of these studies have estimated the impact of tsunamis on populations at relatively small spatial scales, i.e. at one location, or a few sites (Whanpetch *et al*. 2010; Lomovasky *et al*. 2011; Kanaya *et al.* 2015). In such cases, the stochastic effect of selecting a site for sampling, which strengthens the influence of local coastal topography on the wave impact of the tsunami (Wijetunge 2006; Mori *et al*. 2011), can become too large to obtain a general picture of

regional-scale impacts of the tsunami. Third, most studies have estimated tsunami damage on the basis of (1) changes in abundance based on a comparison between data from two sampling times (before and after the impact), or (2) comparison between abundance data from impact and control sites, obtained after the tsunami in a snapshot sampling (e.g. Paterson *et al.* 2012, Urabe *et al.* 2013). In the former case, any population difference detected between before and after the event will inevitably include the effects of environmental and demographic stochasticity as well as the tsunami effects. In the latter case, spatial differences in abundance will reflect not only the tsunami effects but also the spatial variation of environmental factors. Ideally, tsunami damage on a focal community should therefore be evaluated on the basis of its influence on many species randomly selected from the focal community. In addition, the tsunami impact on populations of the selected species should be estimated over a large spatial scale encompassing the entire metapopulation. Furthermore, changes in abundances between before and after the tsunami, as an indicator of the tsunami impact on each species, should be standardized to population variability under normal conditions for each species. To our knowledge, however, no previous studies have met these conditions.

The Great East Japan Earthquake occurred on 11th March, 2011, triggered a mega-tsunami (the 2011 Tohoku earthquake tsunami) with a run-up height that reached 40 m (Mori *et al*. 2011; 2012). Although mega-tsunamis are rare events with a return period of multiple decades at a regional scale (Dominey-Howes 2007; Usami 2013), they occur almost every year somewhere in the world (Lander *et al.* 2003; Scheffers & Kelletat 2003). Mega-tsunamis should have negative impacts on rocky intertidal communities, as expected for other coastal communities; however, the following two basic questions remain unanswered with regard to these impacts. The first question, which has not yet been precisely answered for all coastal communities, is whether tsunamis significantly decrease species population abundances in the rocky intertidal community. The second question is whether there are any differences in the magnitude of tsunami impacts between sessile and mobile species, two major components of the community. Mobile species are generally predicted to be more vulnerable, and to be more easily dislodged by hydrodynamic forces, than sessile species (Denny 1985; 1993; 1995).

For 8 years before the 2011 Tohoku earthquake tsunami, a research group which I belong regularly performed community censuses targeting all macrobenthic species at

23 sites along over 30 km of shoreline located 150–160 km north-northwest of the earthquake epicenter (Okuda *et al*. 2004; Nakaoka *et al.* 2006; Fukaya *et al.* 2010; Munroe & Noda 2010). The biological data obtained in these censuses satisfied all conditions necessary for accurate evaluation of the ecological impacts of the tsunami, as mentioned above. Our purpose here was to evaluate the impacts of the 2011 Tohoku earthquake tsunami on species abundances in the rocky intertidal metacommunity in our census area. Although this earthquake triggered not only tsunamis but also subsidence, this study focuses on effects of tsunamis alone by excluding those of subsidence from overall effects of earthquake. I address the following question: did the tsunami significantly reduce the species abundances of the community as a whole, or of two subgroups, sessiles and mobiles? For this purpose, I evaluated an indicator of tsunami impact, namely the change in mean abundances between before and after the tsunami (as standardized against population variability before the tsunami), for each of five sessile and six mobile species. From this I obtained, as averaged values, quantitative measures of the 2011 Tohoku earthquake tsunami's impact at community-wide level and on the two subgroups. These results allow me to discuss the actual impact of the tsunami on the rocky intertidal community at a regional scale.

2.2 Materials and Methods

Study area

Our study sites were located along 30 km of shoreline on the Sanriku Coast (39°N, 142°E). Our study sites suffered effects from the large tsunamis, with a local height of 8 to 15 m, and from coseismic subsidence (Haraguchi and Iwamatsu 2011). The tidal range at our study sites, defined as the vertical extent between mean high water and mean low water of spring tide, was approximately 140 cm. Commonly found at our study sites were various rocky intertidal organisms, including sessiles such as mussels, barnacles, and perennial algae, and mobile invertebrates such as herbivorous gastropods (Nakaoka *et al.* 2006). These species showed zonation, as evidenced by a vertical distribution with a peak abundance at an intermediate position within a vertical range of several tens of centimeters. Judging from dispersal distances (Kinlan and Gaines 2003), the horizontal

extent of our study sites, encompassing a 30-km shoreline, covered an entire range of metapopulations of most rocky intertidal organisms.

Census design

Abundances of rocky intertidal organisms were monitored at 23 sites from 5 shores along the Sanriku Coast. Distances between neighboring shores ranged from 4.1 to 25.7 km. At each shore, 4 or 5 sites were haphazardly chosen from among semi-exposed locations. In July 2002 at each site, a permanent plot was marked with plastic anchors drilled into roughly vertical rock delimiting a study area that was 50 cm horizontally by 100 cm vertically, centered at the mean tidal level. Distances between neighboring plots ranged from 7.8 to 172.5 m (mean ± SD, 49.4 ± 48.3 m). The vertical extent of the permanent plots covered 72.4% of the tidal range. In March 2011, the census area experienced subsidence of around 50 cm due to the Great East Japan Earthquake. In July 2011, I therefore vertically extended the permanent plot at each site (an additional 100 cm high by 50 cm wide), with the lower border of the new part of the plot sharing the top border of each original permanent plot, so that the vertical observation range was 200 cm.

Permanent plots were monitored at low tide in July from 2003 to 2011. At each census, the abundance of each mobile species was estimated in each 50 cm wide by 10 cm high band of the 10 (before tsunamis) or 20 (after tsunamis) quadrats, representing vertical sections of each permanent plot. In addition, the coverage of each sessile species was estimated by a point sampling method, counting the occurrence of the focal species at 20 points on a grid superimposed on each plot with 5-cm intervals both vertically and horizontally.

To estimate the vertical subsidence at each shore, I measured the vertical deviations of seawater level from the height of anchors drilled at the mid-point of each permanent plot in July 2011, May 2012 and July 2012, assuming a measurement precision of 5 cm based on our minimum sampling resolution of the vertical distribution of the sessile species. I then used the measured deviations and tide level data from the Japan Meteorological Agency to estimate the vertical subsidence as 50 cm at four shores (Myojin, Oura, Aragami, and Katagishi) and 60 cm at Akahama.

Data analysis

Estimation of species-level tsunami impacts

The Great East Japan Earthquake caused subsidence of around 50 cm as well as subsequent tsunamis in the study area; therefore, the abundances and vertical profiles of rocky intertidal organisms could have been altered not only by the tsunamis but also by the subsidence. The subsidence would have resulted in an immediate 50- or 60-cm downward shift in the distribution of all sessile organisms without changing their abundances. Therefore, our estimated changes caused in the abundances of sessiles by the tsunami needed to be based on a comparison of abundances as measured within the borders of the plots established in 2002. In contrast, all mobile organisms would have been able to return to their original elevational ranges right after the subsidence, because the vertical range of subsidence was narrower than the daily tidal range. Therefore, our estimated changes caused in the abundances of mobiles by the tsunami needed to be based on a comparison of abundances measured within the same elevational range (between 50- or 60- cm above and 50- or 60- cm below mean tidal level) within the same plot.

To estimate the impact of the tsunami on the abundance of each species, I first calculated the annual population growth rates for sessile and mobile organisms. For the years before the tsunami (2003–2010), the annual population growth rates r_t (from year *t–1* to year *t*) were calculated as the log ratio of densities (Royama 1992):

$$r_t = logN_t - logN_{t-1} \quad (1),$$

where N_t is the mean abundance per plot in year *t*, obtained as the mean coverage or the mean density in permanent plots of sessile and mobile species, respectively. For growth between 2010 and the year of the tsunami (2011), the population growth rates of sessile species were obtained by subtracting the logarithm of mean coverage per plot in 2010 from the logarithm of mean coverage in 2011 measured within the range of the plots established in 2002; the population growth rates for mobile species were obtained by subtracting the logarithm of mean abundance per plot in 2010 from the logarithm of mean density in the same elevational range (between 50 cm above and 50 cm below mean tidal level) in 2011.

By using annual population growth rates r_t, I then obtained the no assumption effect size of single-subject data (Busk & Serlin 1992; Olive & Smith 2005; Petursdottier *et al*. 2009; Hurwitz *et al.* 2015), ES_i, representing the impact of the tsunami on species i, as calculated by dividing the difference between each species' baseline and

intervention-phase means by the standard deviation of the baseline (Glass 1976; Busk & Serlin 1992; Busse *et al*. 1996):

$$ES_i = \frac{r_{i,2010-2011} - \bar{r}_{i,before}}{SD(r_{i,before})} \quad (2).$$

Here, $r_{i,2010-2011}$ and $\bar{r}_{i,before}$ represent the population growth rate from 2010 to 2011 and the mean annual population growth rate in the pre-tsunami period for species i, respectively, and $SD(r_{i,before})$ denotes the standard deviation of the annual population growth rate in the pre-tsunami period for species i.

Estimation of community-level tsunami impacts

I evaluated the impact of the tsunamis on the whole community and on two subgroups: sessiles and mobiles. I calculated the mean effect size ($\overline{ES}$) for each group by simply averaging the effect size for species (ES_i) that were included in each group (Glass 1976; Busk & Serlin 1992; Hurwitz *et al.* 2015):

$$\overline{ES} = \frac{\sum_{i=1}^{n} ES_i}{n} \quad (3).$$

Here, n denotes the number of species included in each group. The 95% confidence intervals for mean effect sizes ($\overline{ES}$) were generated by bootstrapping, corrected for bias in unequal distribution around the original value by using the bias-corrected and accelerated (BCa) method (Busk & Serlin 1992; Kirby & Gerlanc 2013).

Our dataset contained 75 sessile and 38 mobile species. Among them, I selected five sessile and six mobile species (Table 2-1) for calculating ES_i to ensure the accuracy of $\overline{ES}$, the community-level effect of tsunamis alone, using five criteria. First, I selected species for which the abundance and distribution seemed unaffected by the subsidence. For sessile species, I obtained an ES_i based on a comparison of abundances within the ranges of plots established in 2002. However, for some sessile species, the vertical distribution might have changed between the time of the tsunami and the post-tsunami survey (4 months after the earthquake), through mortality caused by transport below their normal vertical range by subsidence or through recruitment into the normal vertical range following subsidence. Such species therefore needed to be eliminated from estimates of direct tsunami impacts. To detect such species, I visually determined whether the vertical profiles of their abundances within the range of plots established in 2002 clearly changed

from 2010 to 2011 for each species. This was because such changes in vertical profiles would have been quite sensitive to mortality or recruitment, which in turn would have been strongly dependent on the elevation after the subsidence. For mobile species, I obtained an ES_i based on a comparison of abundances measured within the same elevational range (between 50 cm above and 50 cm below mean tidal level) in the same plot. However, the vertical distribution of some of these species might have changed after the subsidence, because the vertical distributions of some sessile organisms, which provide food or microhabitat for mobiles, might have been changed by the subsidence. Therefore, such species needed also to be eliminated from estimates of the tsunami impacts. To detect such species, I visually determined, for each species, whether the vertical profile of abundance within the same elevational range (between 50 cm above and 50 cm below mean tidal level) clearly changed from 2010 to 2011. Second, I eliminated those species for which abundance increased after the subsidence, because the tsunami could not have directly increased abundance—it could only have decreased it. I applied a paired *t*-test to each species to determine whether its abundance increased from 2010 to 2011 within the same original 2002 plot (in the case of sessile species) or in the same elevational range (in the case of mobile species).

Third, I selected species that had been observed in all years. This was because inclusion of any years without observations would have reduced the sample size used to estimate the mean and standard deviation of population growth rates during the pre-tsunami period, and thus would have reduced the accuracy of the estimated tsunami impacts.

Fourth, I selected species for which the pre-tsunami mean total coverage value was at least 0.007 (for sessile species), or for which the number of individuals each year in permanent plots was more than 30 (for mobile species). This was because estimates of population growth rates in species with small population sizes would have included an observation error too large to obtain a general picture of the population-level impact of the tsunami.

Fifth, I selected those species for which the mode of the vertical distribution of abundance was located within the vertical range of the permanent plot. This is because the population dynamics of rocky intertidal organisms often vary across their elevational range (e.g. Fukaya *et al*. 2014); therefore, any estimated tsunami impact near the limits

this range might not reflect impacts across the entire elevational range. To select appropriate species, I first obtained the mean number of individuals (for mobile species) or the mean coverage (for sessile species) for each of the ten 10 cm × 50 cm quadrats covering the vertical range of each plot. These mean values were calculated by using data from all plots in all years before the tsunami. I then visually judged for each species whether or not the vertical abundance distribution profile was unimodal.

2.3. Results and Discussion

The 2011 Tohoku earthquake tsunami had a significant negative impact on the rocky intertidal community at the regional scale (Fig 2-1), with a decline in abundance of 11 species by 45.25% on average (Table 2-2). Unfortunately, this decrease cannot be simply compared with population declines caused by other disturbance events at similar large spatial scales, such as oil spills or massive ice-scours, because the ecological impacts of such events have rarely been quantified and have not yet been reported for the community level at regional scales (Moyse & Nelson-Smith 1964). However, several reports indicate that such large-scale disturbances cause catastrophic damage to many species on intertidal rocky shores. For example, the *Torrey Canyon* oil-spill incident in 1967 resulted in the disappearance of almost all limpets, carnivorous snails, calcareous algae, and kelp from the rocky intertidal shore along tens of kilometers of shoreline around Cornwall, England (Southward & Southward 1978). Furthermore, a massive ice-scour of the rocky intertidal seashore in Canada in 1987 removed almost all barnacles and mussels and the macroalga *Fucus* sp. from more than 50 km of exposed rocky shoreline (McCook & Chapman 1991; 1997). These reports on an oil spill and a massive ice scour impacts and this study involve a similar length of the time lag between the event and post-event survey (i.e. 2–4 months), which may cause the subequal underestimation of the direct negative impact through the population recovery for these studies. Thus the impact of these large-scale disturbances on rocky intertidal communities seems larger than the negative impact of the tsunami caused by the megaquake.

The tsunami did not have a significant negative impact on sessiles, but it did on mobiles (Fig 2.1). This suggests that mobiles are more vulnerable to tsunamis than

sessiles on rocky shores. Indeed, in the Alaska earthquake of 1964, populations of mobiles (limpets *Acmaea persona* and *Acmaea digitalis*) declined along rocky intertidal shores after the resultant tsunami, whereas the species composition and zonation of rocky intertidal sessile assemblages did not clearly change except in the area of heavy uplift (Haven 1971). Following the Philippines earthquake tsunamis in 2004, there were no reported changes in abundance of any rocky intertidal sessile species, but there were decreases in the abundance of the intertidal littorinid snails *Littoraria undulata* and *Echinolittorina feejeensis* after the tsunami (Sanpanich *et al.* 2006). In addition, the 2011 Tohoku earthquake tsunami caused decreases in populations of the abalone *Haliotis discus* by about 50%, whereas populations of the kelp *Eisenia bicyclis* did not clearly decrease on subtidal rocky shores (Takami *et al*. 2013).

The decrease in populations of mobiles caused by the 2011 Tohoku earthquake tsunami could have affected the abundances of their prey species and consequently could alter the community structure via indirect interactions for decades, because community structure on the intertidal rocky shore is often strongly influenced by top-down effects (Lubchenco & Gaines 1981; Menge 2000). Indeed, previous studies have documented that disturbance events with spatial scales similar to that of the tsunami reduce the populations of mobile invertebrate consumers and consequently alter the rocky intertidal community structure for decades. The decrease in populations of the limpet *Patella vulgate* caused by the *Torrey Canyon* oil-spill incident triggered unusual growth of the green algae *Enteromorpha* and *Ulva*, preventing recovery of barnacle populations for more than 10 years (Southward & Southward 1978). The *Exxon Valdez* oil spill reduced populations of molluscan grazers (limpets and periwinkles) and carnivorous gastropods (whelks). The declines in populations of these consumers triggered blooms of ephemeral green algae and an opportunistic barnacle, *Chthamalus dalli*, which inhibited the recovery of *Fucus* sp., lengthening the recovery process on rocky shorelines in Alaska for decades (Peterson *et al.* 2003). In addition, a massive ice-scour event in Canada in 1987 also reduced numbers of the molluscan grazers *Littorina obtusata* and *Littorina rudis* and the predatory whelk *Nucella lapillus*. Their declines facilitated the recruitment of ephemeral green algae and mussels, consequently inhibiting the establishment of the perennial seaweed *Fucus vesiculosus*—which was a dominant sessile species before the massive ice-scour event—for almost a decade (McCook & Chapman 1991; 1997).

2.4. Conclusions

Although it has been widely assumed that tsunamis can severely damage coastal ecosystems, our study strongly suggested that the rocky intertidal community at a regional scale suffered significant but only relatively minor direct damage from the tsunami caused by the Great East Japan Earthquake in 2011 than other catastrophic events such as oil spill (Southward & Southward 1978) and massive ice scour (McCook & Chapman 1991; 1997). This gap between actual and assumed impacts asserts the primacy of exact quantification in ecological consequences of disturbance. The approach used here should be applicable to quantification of the direct influence of a variety of disturbance events on various communities.

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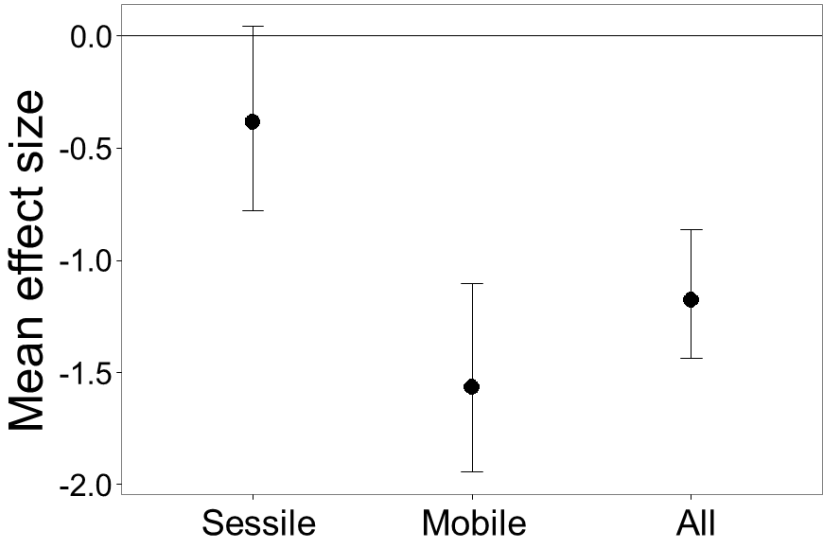


Fig 2-1. Mean effect size of tsunami impacts on the abundance of all species combined and on two subgroups in the rocky intertidal community. Vertical lines denote bias-corrected 95% confidence intervals, which were generated by bootstrapping procedures (10,000 iterations). The zero line indicates no effect, and mean effects are considered significant when the 95% confidence interval does not cross the zero line.

Table 2-1. Species used for estimating the tsunami impact.

Species		Taxonomic group	Trophic group
Sessile			
	Analipus japonicus	Phaeophyceae	Primary producer
	Hildenbrandia rubra	Florideae	Primary producer
	Crassostrea gigas	Bivalvia	Suspension feeder
	Chthamalus challengeri	Crustacea	Suspension feeder
	Mytilidae spp.	Bivalvia	Suspension feeder
Mobile			
	Cellana grata	Gastropoda	Herbivore
	Lottia kogamogai	Gastropoda	Herbivore
	Lottia lindbergi	Gastropoda	Herbivore
	Lottia tenuisculpta	Gastropoda	Herbivore
	Monodonta confusa	Gastropoda	Herbivore
	Notoacmea fuscoviridis	Gastropoda	Herbivore

Table 2-2. Mean population growth rates for each group in the year of the tsunami.

Group	Population growth rate Mean ± SE (log_{10})
All	–0.26 ± 0.14
Sessile	0.04 ± 0.05
Mobile	–0.45 ± 0.23

Chapter III

A framework for quantifying the relationship between intensity and severity of impact of disturbance across types of events and species

3.1. Introduction

Understanding the impacts of natural disturbances, such as hurricanes, droughts, heat waves, severe cold events, volcanic eruptions and tsunamis on wildlife populations is a central task for ecologists (Sousa 1984; Overpeck *et al.* 1990; Gardner *et al.* 2005; Pickett & White 1985: Turner 2010). In general, the 'severity' of impact of a disturbance, often measured as the percentage mortality of a population or kilograms of biomass removed (Pickett & White 1985; Walker 2012), is likely to depend primarily on the 'intensity' of disturbance, which I define as the strength of the disturbing force, such as moment magnitude (Mw) for an earthquake or wind speed (m/s) for a hurricane (Pickett & White 1985; Walker 2012). In addition, severity can vary with the type of disturbance (e.g., earthquake, hurricane, or heat wave) and the degree of vulnerability of the species (Pickett & White 1985). Thus, to understand disturbance severity, it is crucial to examine how severity increases with increasing intensity, and how the relationship varies across different disturbance types or species (Sousa 1984; Pickett & White 1985: Turner 2010).

White and Jentsch (2001) discussed the need to identify the general patterns of severity of natural disturbances across species and event types. Peters *et al.* (2011) proposed a conceptual framework to quantitatively compare disturbance effects across

different types of ecosystems and disturbances, and Fey *et al.* (2015) evaluated the temporal pattern of the magnitude of effect (number of deaths) and the frequency of various types of disturbance event for various taxa. However, to our knowledge, no study has quantified both intensity and severity across different types of disturbance and species and evaluated the severity–intensity relationship comprehensively. Such an analysis is hindered by two main obstacles. First, differences in the physical units of the force strength among disturbance events (e.g., wind speed for hurricanes and moment magnitude for earthquakes) make it impossible to directly compare intensity between different disturbance types. Second, interspecific differences in the temporal variability of population size under normal (non-disturbance) conditions make it impossible to use the change in abundance after a disturbance event as a measure of severity: that is, observed population changes might not be caused by the disturbance effect alone, but also by the species-specific natural variability in abundance.

To solve these problems, I devised an analytical method that uses two different dimensionless parameters for 'return period' to characterize both the intensity of a disturbance and the severity of its impact. I define the return period for the intensity of a disturbance as the average interval between occurrences of an event with a given force strength in a particular physical unit. In the case of climatic events, the return period is the inverse of the occurrence probability of that event. In the case of rare or occasional events such as tsunamis, the return period is the length of the recording period divided by the number of events of similar magnitude. To calculate a return period for the severity of impacts, I first calculate the effect size of the disturbance on the annual population growth rate, with the annual population growth rate calculated as the logarithm of the ratio of abundance in two consecutive years. This effect size reflects the difference between the annual population growth rate under normal conditions and the rate in the year when the disturbance event occurred. I then calculate the return period as the inverse of the occurrence probability of the effect size calculated above. This return period represents the severity. (See Appendix Fig. A3-1.)

With these new measures, I performed a meta-analysis to examine severity–intensity relationship of the impact of different types of disturbance on various species (see Appendix Tables A3-1 and A3-2). When examining the causal relationship between intensity and severity, I used only intensity to detect disturbance events (Jentsch *et al.*

2011). I focused on the severity impacts of large-scale (≥10 km^2) disturbance events that had extreme intensity values (Zscheischler *et al.* 2013) and occurred in ≤5% of years or less (≥20-year return period). The hypothetical species experienced such events no more than once in two generations (generation time ≤10 years). Large-scale and infrequent disturbances—relative to the body size and generation time of affected species—are ecologically important owing to their large extents and the persistent damage they cause to populations (Turner & Dale 1998); however, our ecological knowledge of such events is poor because observations of them have been limited (Turner & Dale 1998; Smith 2011; Wernberg *et al.* 2013; Gaines & Denny 1993). In addition, I excluded species with a generation time of less than 1 year, because such species tend to have very high population growth rates and there is a high risk that the growth and reproduction occurring immediately after the disturbance could mask the damage at the first census after the event and thus lead to underestimation of the severity. To assure the accuracy of my estimation of the severity of such events, I carefully selected populations with sufficient quality of abundance data for the analysis (see Methods; Appendix File A3, section 1; and Appendix Tables A3-1 and A3-3).

Intensity—a measure of the force of disturbances—generally follows either a normal or an extreme temporal distribution (Smith 2011; Gaines & Denny 1993; Katz *et al.* 2005). The return periods of more intense events are represented as becoming longer owing to lower occurrence probabilities in the lower, upper, or both tails of the frequency distribution (Gaines & Denny 1993; Katz *et al*. 2005). (For details, see Methods and Appendix Fig. A3-1a.)

To quantify severity, I assessed the impact as an effect size, which is represented as the change in annual population growth rate between the year when the disturbance event occurred and under normal conditions.

The effect size was calculated while accounting for single-subject data (i.e., the event occurred once, so the treatment data show no variability, whereas the control data were gathered over multiple years and do show variability) (Busk & Serlin 1992; Olive & Smith 2005; Petursdottir *et al*. 2009; Hurwitz *et al*. 2015), as follows (Busk & Serlin 1992; Glass 1976; Busse *et al*. 1996):

$$ES_i = \frac{r_{i,\mathrm{pd}} - \bar{r}_{i,\mathrm{n}}}{SD(r_{i,\mathrm{n}})} \quad (1)$$

where $r_{i,\mathrm{pd}}$ represents the annual population growth rate of species *i* in the year when the disturbance event occurred and $\bar{r}_{i,\mathrm{n}}$ represents the mean annual population growth rate of the same species under normal conditions, and $SD(r_{i,\mathrm{n}})$ denotes the standard deviation of the annual population growth rate under normal conditions for species *i*. The return period of a given severity was calculated as the inverse of the occurrence probability of a given effect size, which was estimated statistically while assuming a normal distribution. (For details, see Methods and Appendix Fig. A3-1b.)

To examine the relationship between intensity and severity, I gathered more than 8000 time series of population abundance from the literature. I then strictly examined whether each dataset satisfied the selection criteria for accurately quantifying the severity of disturbance events. (For details, see Appendix File A3, section 1; Appendix Table A3-3 online.) From this selection, I quantified the intensities of 27 disturbance events representing five types of disturbance and the severities of their effects on the populations of 50 species across a wide range of taxa (eight classes: Mammalia, Aves, Insecta, Crustacea, Bivalvia, Phaeophyceae, Florideophyceae and Phaeophyceae) with generation times ranging from 1 to 10 years, using data from 17 studies (including three unpublished studies; see Appendix Tables A3-1 and A3-2).

3.2. Methods

Here, I describe the steps in the analysis of the relationship between the intensity of various types of disturbance and the severity of impact on various species. First, to estimate the severity of the impact of various disturbance types on species, I collected high-quality time series of population abundance. Second, by using time series of measured disturbance intensity or historical evidence of a focal disturbance event, I estimated the return period of disturbance intensity in the period during which abundance was surveyed. I then extracted the time series of abundance for populations that experienced a disturbance event with an intensity return period of ≥20 years. Third, I estimated the severity of the impact of the disturbance event by comparing the population growth rate in the year the disturbance occurred with that under normal conditions. Finally, I statistically analyzed the severity–intensity relationship from 27 disturbance events of

five types.

Time series of abundance

To quantify the severity for various species of various disturbance events with a ≥20-year return period of intensity, I obtained primary time series for the abundance of populations affected by such events during the study period (8–42 years) from three sources: (1) Google Scholar; (2) the Global Population Dynamics Database (ver. 2); and (3) our long-term research study of a rocky intertidal shore. The sources and search strategy are described in Appendix File A3, section 1.

The time series obtained for abundance were pre-processed as needed. From among the pre-processed time series, I then extracted those that satisfied the basic requirements for use in the analysis. Details of the procedures are given in Appendix File A3, section 1.

Disturbance event intensity

Calculation of the return period of intensity

The return period of intensity was calculated by using two different methods, depending on the type of disturbance event, namely (1) a climatic disturbance event (e.g., severe winter or drought); or (2) an occasional or rare disturbance event (e.g., tsunami) (see Appendix Figure A3-1a). For a climatic disturbance event, the physical measure of intensity was recorded annually as the environmental fluctuation, such as the deviation from mean temperature for a severe winter or deviation from mean precipitation for a drought. I statistically estimated the return period of intensity as the inverse of the occurrence probability of the focal disturbance event per year by using long-term time series of force-strength measurements. The occurrence probability of the force strength was assumed to follow either a normal distribution (Schär *et al.* 2004) or a general extreme distribution (Gaines & Denny 1993; Katz *et al.* 2005). The occurrence probability of the force strength will follow a normal distribution when the measure is represented by the average or cumulative value (e.g., average temperature or cumulative precipitation). Before assuming a normal distribution, I tested the normality of the data distribution by using the Shapiro–Wilk W-test. I transformed the data to follow a normal distribution (e.g., by using logarithms) when the assumption was not valid. The

occurrence probability of force strength will follow a general extreme distribution when the measure is represented by the maximum or minimum value or a value based on a threshold (e.g., the maximum wind speed or the number of days with >5 cm of snow depth). In both cases, the distribution parameters were estimated from the observed data by using maximum-likelihood estimation. The return period of the event was then calculated from the fitted distribution (Schär *et al.* 2004).

For an occasional or rare disturbance event, the physical measure of the intensity was not recorded annually (e.g., wave height for a tsunami). Therefore, I estimated the return period of intensity as the average interval of occurrence in the reference data of such an event with equal or greater intensity (Ishimura & Miyauchi 2015). The interval was estimated by extrapolation based on historical evidence of the event rather than by using direct observational data such as sediment deposits (Goff *et al.* 2001). For each selected time series of abundance, the intensity of the disturbance event was estimated by using the procedure described in Appendix File A3, section 2.

Estimation of severity

Calculation of the return period of severity and annual population growth rates

For each species, the return period of severity was calculated on the basis of the effect size on the annual population growth rate in the year when the disturbance occurred by using equation (1) for each selected time series of abundance. (See also Appendix Fig. A3-1b online.) The return period representing a given severity was calculated as the inverse of the occurrence probability of a given effect size, which was statistically estimated assuming a normal distribution.

To estimate the effect size of severity, I calculated the annual population growth rates under normal conditions and those in the year the disturbance event occurred in each selected time series (Appendix Fig. A3-1b). To calculate these population growth rates, I obtained 1-year interval time series of abundance, as follows. If multiple abundance measures were made within each year, I selected a single value measured in the same season as the first census conducted after the focal disturbance event. Then abundances with an average value of zero were treated as missing data.

The annual population growth rates under normal conditions, which were defined as those not influenced by the focal disturbance event or other events or stresses

such as anthropogenic disturbances, were calculated as follows. First, if it was reported in the original literature that the time series were influenced by such other events or stresses during part of the recording period, I excluded the abundance data during that period from the analysis. Second, if the focal disturbance event influenced the abundance data measured not only immediately after the event but also in subsequent years, I excluded the abundance data during that period from the analysis to minimize, as much as possible, the bias of the indirect influence of the event on estimated severity. For example, an exponential increase in abundance subsequent to a population decline can be indirectly caused by the disturbance event. To detect the temporal trend in abundance that seemed to be caused by the indirect effect of the focal disturbance event in part of the second and subsequent annual abundance data collected after the event, I examined the relationship between abundance and year by using linear regression. If the temporal trend in abundance was significant ($P<0.05$), I excluded data influenced by the indirect effect of the focal disturbance event by removing data beginning with the oldest census; I included in the analysis only the part of the annual abundance data that did not represent the significant temporal trend.

The population growth rate in the year the disturbance event occurred was calculated by using the two abundance measures recorded immediately before and after the disturbance event. If a disturbance event drove the mean abundance of an population to zero immediately after the event, then the effect size, as the basis of severity, should be calculated by using the abundance plus a small number in order to avoid an infinite value (i.e., to prevent division by zero); however, the database I used for the meta-analysis did not include such cases. The detailed procedures to estimate the severity of the effect of a disturbance are described in Appendix File A3, section 3.

Statistical analysis

The relationship between $\log_{10}$ of the return periods of intensity and severity was analyzed by using a generalized linear model, taking severity as the response variable and intensity as the explanatory variable. The error distribution and link function in the generalized linear model were based on the value of Akaike's information criterion and the Schwarz Bayesian information criterion for each potential model (the model with the smallest value was chosen); this resulted in gamma-distributed errors with a log-link function (see

Appendix Table A3-4). All analyses were performed with version 3.02 of the R programming language (www.r-project.org) (R Development Core Team 2013).

3.3. Results and Discussion

Severity increased exponentially with intensity (Fig. 3-1a; $P = 6.35\times10^{-6}$): the return period was smaller for severity than for intensity up to an intensity return period of 61 years ($\log_{10} = 1.8$). For disturbances less frequent than that, the return period of severity was greater than that of intensity. Thus, populations could decline more in response to physically intense events occurring less frequently than twice in a century than expected from the relationship for physically weak but frequent events. This result may reflect the fact that a higher frequency of disturbance relative to the life span of an organism must exert strong selection pressure on species to evolve disturbance resistance (Sousa 1984; Harper 1977; LaJeunesse *et al.* 2010; Mitchell-Olds & Schmitt 2006).

The severity–intensity relationship (Fig. 3-1a) also shows that the 95% confidence interval of severity dramatically increases with increasing intensity. In addition, the two largest deviations of severity from the regression curve were for those disturbances with return periods for intensity of >100 years (Fig. 3-1b). These findings indicate that although intense and rare disturbances could cause catastrophic decline of populations of the most vulnerable species, the damage to other components of communities would vary. Therefore, reliable prediction of the ecological consequences of intense and rare disturbances will require knowledge of the species traits determining disturbance susceptibility, the population recovery processes such as reproduction of surviving individuals and recolonization, and the community importance (Power *et al.* 1996) of species that are highly susceptible to rare disturbances.

To demonstrate how the severity–intensity relationship differs among species traits, we used species mobility to split our dataset into two groups and then reanalyzed the data. A significant positive relationship between intensity and severity was obtained for mobile species, but not for sessile ones (Fig. 3-2). Unfortunately, because of bias in habitat between the two species groups, we could not say that this difference in the severity–intensity relationship depended on the mobility of organisms: all sessile species

are rocky intertidal organisms, whereas all mobile species are terrestrial organisms. Therefore, because of the small sample size for each event and bias in the habitats of the species groups, we could not evaluate how the severity–intensity relationship was influenced by event types and species traits in this analysis. In particular, event types are closely related to the habitat and traits (e.g., morphology or life history) of organisms, so that the combination of disturbance types and species traits is likely to have limited variation in the available data. For example, heavy snowfall will likely affect only those species in snowy regions and tsunamis will likely affect only coastal species. Analyzing the effects of event type and species traits on the severity–intensity relationship requires not only an adequate number of samples but also variation in species traits and event types and intensities in each habitat analyzed.

Our findings help to explain a surprising feature of the severity–intensity relationship for a particular event. Unexpectedly, the severity of the mega-tsunami caused by the March 2011 earthquake off the Pacific coast of Tohoku was relatively small for rocky intertidal benthic organisms, despite the high intensity of the disturbance (Ishimura & Miyauchi 2015) (Fig. 3-1b). The relatively low severity of the effect of the tsunami might be related to the tsunami's short duration (Japan Meteorological Agency 2012; Mori *et al.* 2012) because the magnitude of the impact of wave force on rocky intertidal benthic organisms is related to the duration (Denny 1995). For example, a storm occurred along the pacific coast including Tohoku region in 2006, and its intensity was one order lower than that of the 2011 tsunami but its duration (a few days) was an order of magnitude longer than that of the tsunami (a few hours). The severity of the effect of the storm on the same species in the same region of rocky intertidal shore was of the same order as that of the tsunami (Table 3-1). Thus, duration is also an important determinant of the severity of natural disturbance events (Sousa 2001). Before assessing the effect of duration on severity, we should examine the relationship between intensity and duration. This is because intensity in some disturbances is defined independently of duration, but in others in terms of it. In the former, we can include duration directly in the analysis as an explanatory variable for severity (e.g., earthquakes: seismic intensity). The latter has two cases: when duration is synonymous with intensity (e.g., severe winters: number of days > 5-cm snow depth), we cannot include duration in the analysis, but when duration is correlated with intensity (e.g., severe winters: maximum snow depth), we can include

a composite variable of duration and intensity obtained by principal component analysis.

I found that the mean and variance of severity increase exponentially with increasing intensity. From a conservation perspective, it is crucial to predict the severities of physically intense events that occur less than twice in a century and may cause population decline disproportionate to the intensity because of a species' poor disturbance resistance. However, the severity of the effect of such events cannot be extrapolated from the severity–intensity relationship derived from data for physically weak and frequent disturbances, the population-level consequences of which have been reported extensively (Sousa 2001; White 1979).

Deciphering the influence of event types and species traits on the severity–intensity relationship would greatly improve our understanding of the role of natural selection and phylogenetic constraints on evolutionary responses to disturbance. It would also allow us to predict the ecological consequences of various kinds of disturbance events of unexperienced intensity, including extreme weather events caused by climate change (Katz *et al.* 2005; Dale *et al*. 1998; Jentsch *et al*. 2007; Scholze *et al*. 2006) at multiple ecological levels (e.g., population, community, and ecosystem). Unfortunately, the current lack of studies and the biased datasets make these analyses impossible, highlighting the urgent need to conduct long-term censuses of various kinds of organisms in different habitats.

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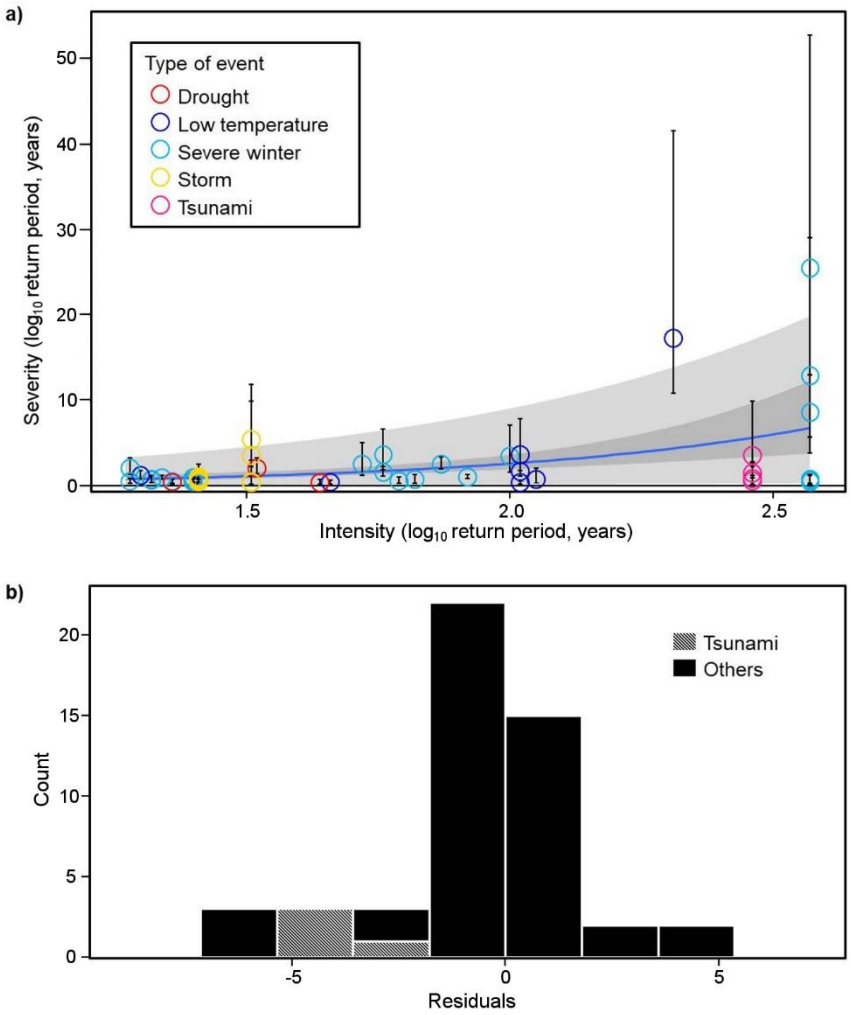


Figure 3-1. The relationship between intensity and severity. (a) The relationship between intensity and severity of 27 disturbance events across five types of disturbance. Each point is a species-level severity value for each disturbance event (n = 50). Vertical lines denote bias-corrected 95% confidence intervals (Busk & Serlin 1992), which were generated by bootstrapping procedures (10 000 iterations) (Kirby & Gerlanc 2013). The blue line represents the estimated mean severity. The darker and lighter shading demarcate the slope of the 95% confidence intervals and 95% prediction interval for future observations, respectively. (b) Variation in the residuals of species-level severity values from a model describing the relationship between intensity and severity using a generalized linear model without taking into account the type of disturbance and species. All four severity values (hatched shading) were detected for tsunamis whose return periods of intensity of about 300 years were relatively small, whereas the two largest residuals of severity were detected for the other two disturbance events with intensity of over 100 years in the return period.

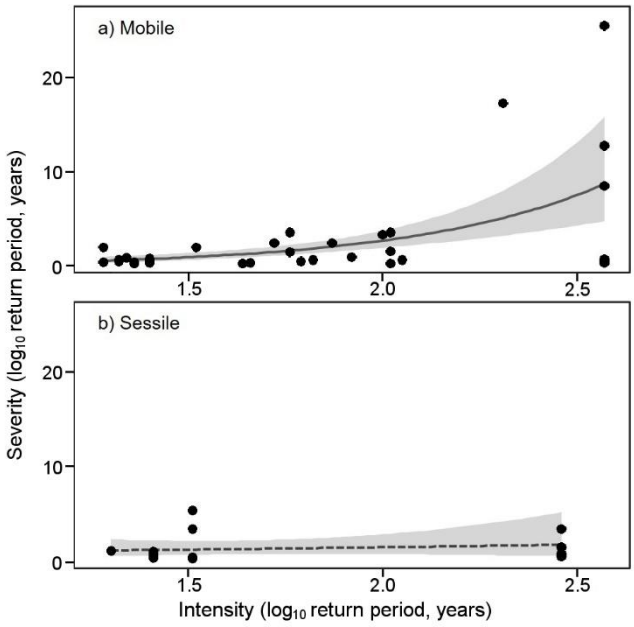


Figure 3-2. An example of the relationship between intensity and severity in (a) mobile and (b) sessile groups. Each point is a single species-level severity value. Lines represent the fitted curve estimated by a generalized linear model, with the solid line statistically significant and the dashed line not. Shading demarcates the slope of the 95% confidence intervals.

Table 3-1. Comparison of the intensity and severity of the impact of a storm in 2006 and a tsunami in 2011 on rocky intertidal benthic organisms in the Tohoku region, Japan. Mean severity is the average of four species-level severity values for each event.

Event	Intensity ($\log_{10}$ return period, years)	Mean severity (± SE) ($\log_{10}$ return period, years)
Storm in 2006	1.51	4.79 (± 4.78)
Tsunami in 2011	2.46	2.88 (± 2.89)

Appendix A3

File A3 Detailed description of methods

1. Time series of abundance

Sources of time series of abundance

To quantify the severity of the effect of various disturbance events with an intensity return period of ≥20 years on various species, I obtained primary time series for the abundance of populations affected by such an event during the study period from three sources: (1) Google Scholar (GS); (2) the Global Population Dynamics Database (GPDD, ver. 2); and (3) our research project along a rocky intertidal shore (RPRI). When searching GS, to gather primary literature by authors self-identifying and reporting the effects of disturbance events on populations I used a keyword search for each of the following terms or their combinations: ("abundance" OR "population size") AND ("natural disturbance" OR "catastrophic event" OR "extreme climate") AND ("impact" OR "decrease" OR "damage"), ("long term"), ("large scale" OR "region*"), ("pre and post" OR "before and after"). I finished conducting our search on 24 December 2014; the search yielded 2940 hits. GPDD is the largest database of population time series and includes >10-year time series for nearly 5000 populations of 1800 species (24 classes, including terrestrial plants, e.g., Dicotyledoneae; terrestrial and aquatic invertebrates, e.g., Insecta and Bivalvia; terrestrial and aquatic vertebrates, e.g., Mammalia and Osteichthyes; and unicellular organisms, e.g., Dinophyceae and Bacillariophyceae) across the globe. In the case of the abundance data obtained from GS and GPDD, I examined whether the time series satisfied requirements for analysis by reading the original papers or books in the subsequent selection processes; I excluded time series for which the literature was not available. RPRI provided 12 years of time series for hundreds of populations of sessile organisms on rocky intertidal shores (e.g., algae, barnacles, and bivalves) in six regions along the Pacific coast of Japan. Within each region (>10 km^2) I chose five shores along the coastline. Within each shore, I established five census plots. Each plot was 50 cm wide by 100 cm high, and the mean tidal level corresponded to the vertical midpoint of the plot on steep rock walls. Detailed descriptions of the study sites and biogeographic features of the area can be found in previous reports (Nakaoka *et al.* 2006; Okuda *et al.*

2004).

Pre-processing of the resulting time series of abundance

The resulting time series of abundance were pre-processed, as needed, to provide a single time series of population abundance that included data measured regularly at 1-year or shorter intervals for each species in each study. If the time series of abundance was represented as plots or graphs, I measured values from the figure by applying quantitative methods to highly magnified images using GSYS2.4 (www.jcprg.org/gsys/2.4/index-j.html). If there were multiple census points within the study site, I used the average abundance across the site. If the recording periods differed among the census points within the study site, I used the data in the period for which (1) the census was conducted at multiple census points and (2) the combination of the census points was consistent.

Quality assessment of the pre-processed time series of abundance and selection of the target species

To extract the time series of abundance that satisfied the basic requirement for use in the analysis, I selected relevant time series from the pre-processed ones on the basis of (1) quality assessment of the time series of abundance and (2) selection of the target species. Quality of the time series was assessed on the basis of the purpose of the study, the resolution of the census, the measurement of abundance, the temporal trend of abundance, the spatial scale of the time series, and the length of the time series (Table A3-3-i). Target species were selected on the basis of the absence of seasonal migration and on generation time (Table A3-3-i). The generation time condition for analysis was determined by the temporal scale of the disturbance. I identified disturbance events with a ≥20-year return period with regard to intensity, so I used species with generation times of ≤10 years, because an event that occurs less than once in two generations can be assumed to be a deviation from the usual environmental fluctuation. Although it would be ideal to equalize the relative length of the return period to the generation time of each species, I could not do this owing to the lack of information on the exact generation times of some species and the limited sample numbers.

2. Disturbance event intensity

For each selected time series of abundance, the intensity of a disturbance event that appeared to decrease the focal species abundance and occurred in the period of the study was estimated by using different procedures, depending on whether the disturbance event had been reported in the original literature of the focal time series (I) or not (II) (see Fig. A3-2-I and Fig. A3-2-II).

I. Estimation of disturbance event intensity when the event was reported in the original literature (Fig. A3-2-I).

When the time series of force-strength measurement was reported in the original literature (Fig. A3-2-I, A), I estimated the distribution of the occurrence probability of the force-strength measurement and then identified the physical intensity of the focal disturbance event reported in the original literature. Next, I estimated the return period of the disturbance intensity as the inverse of the occurrence probability of the focal disturbance event per year. Finally, if the return period of the intensity of the focal disturbance event was ≥20 years, I selected the disturbance event for analysis.

When the time series of force-strength measurement was not reported in the original literature (Fig. A3-2-I, B), I used the following two procedures, depending on whether the focal disturbance was a climatic disturbance event (Fig. A3-2-I, C) or an occasional or rare disturbance event (Fig. A3-2-I, D). For a climatic disturbance event, I obtained the time series of the climatic parameter as the force-strength measurements recorded at the station nearest (<20 km distance) to the focal study site. In climatic disturbance events, the climatic parameter (e.g., snowfall for severe winters and wave height for storms) likely has values similar to those at the study site and the nearby station (Perry & Hollis 2005; Izaguirre *et al.* 2011). I selected and used the time series of the climatic parameter that had been recorded at stations with topographic and geographic conditions similar to those of the site (e.g., flatland or distance from the sea) and that covered the whole period for which the population abundance survey was conducted. If there were multiple available time-series data, I used their average value. After these procedures, I estimated the distribution of occurrence probabilities of the climatic parameter. I then identified the intensity of the disturbance event that occurred in the period when the population abundance survey was conducted and estimated the return period of the disturbance intensity. For an occasional or rare disturbance event, I obtained

historical evidence of the focal disturbance event from other literature. We then estimated the return period of intensity of the disturbance event as the average interval of occurrence of such an event with equal or greater intensity. In both procedures, I selected for analysis those disturbance events with an intensity return period of ≥20 years.

II. Estimation of disturbance event intensity when no disturbance event was reported in the original literature (Fig. A3-2-II).

When a disturbance event was not reported in the original literature (Fig. A3-2-II, A), I identified whether the time series of environmental parameters represented the force-strength of the disturbance. In such cases, I estimated the distribution of occurrence probabilities of the force-strength measurements. I then estimated the force-strength of the disturbance for each year in the period when the population abundance survey was conducted. When the environmental parameters were ones that did not represent force-strength, I identified the main type of disturbance event for the focal species by reading the original report or other literature. When the focal disturbance event was climatic (Fig. A3-2-II, C), before I estimated the distribution of occurrence probabilities of the force-strength measurement, I obtained the time series of climatic parameters measured at the station nearest to the study site. When the focal disturbance event was rare or occasional (Fig. A3-2-II, D), before I estimated the return period of the disturbance intensity, I obtained historical evidence of the focal disturbance event from other literature. In both procedures, I selected for analysis those disturbance events with intensity return periods of ≥20 years.

If the time series of the environmental parameters had not been reported in the original literature (Fig. A3-2-II, B), we identified the main type of disturbance event for the focal species by reading the original report or other literature. The following steps were the same as in Fig. A3-2-II, A and the subsequent procedure.

3. Estimation of severity

To estimate the severity of the effect of a disturbance, we first selected the time series of abundance that satisfied the minimum requirements for calculation of the severity (Table A3-3-iii). Next, I calculated the effect size representing the severity. Finally, I excluded those data for which the estimated effect size was positive, meaning that the annual

population growth rate in the year of the disturbance event was higher than usual. The direct effect of a disturbance event cannot be an increase in population abundance, so a positive effect may indicate that the indirect effect of the event was too large to allow evaluation of the direct effect of the focal disturbance event.

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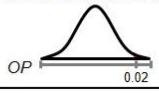
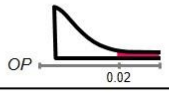
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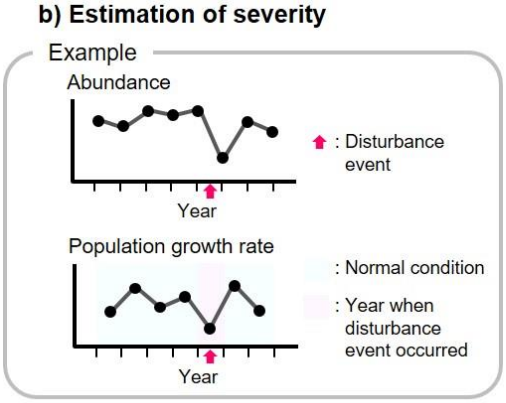
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Izaguirre, C., Méndez, F. J., Menéndez, M., & Losada, I. J. (2011). Global extreme wave height variability based on satellite data. *Geophysical Research Letters*, 38, L10607.

a) Estimation of intensity

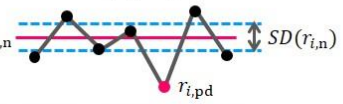
Type of event	Type of data used for calculation	Formula of return period of intensity	Distribution type followed by occurrence probability	Example of data
Climatic event (e.g., severe winter)	Time series of climatic parameter	$\frac{1}{\text{occurrence probability}}$	normal distribution 	total snowfall
			general extreme distribution 	maximum snow depth
Rare or occasional event (e.g., tsunami)	Historical evidence	$\frac{\text{length of recording period}}{\text{number of such events}}$	–	tsunami height

b) Estimation of severity



Effect size of disturbance severity (ES_i)

$$ES_i = \frac{r_{i,\mathrm{pd}} - \bar{r}_{i,\mathrm{n}}}{SD(r_{i,\mathrm{n}})}$$



$r_{i,\mathrm{pd}}$: annual population growth rate (gr) in the year when the disturbance event occurred for species i (SP_i)

$\bar{r}_{i,\mathrm{n}}$: mean gr under normal conditions for SP_i

$SD(r_{i,\mathrm{n}})$: standard deviation of gr under normal conditions for SP_i

Return period (RP) of severity

$$= \frac{1}{\text{occurrence probability } (OP) \text{ of } ES_i}$$

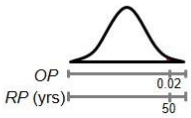


Figure A3-1. Diagram of estimation of intensity and severity. (a) Intensity was estimated by two different methods depending on the type of disturbance event: climatic events and rare or occasional events. Intensity was represented by the return period, which was estimated as the inverse of the occurrence probability for climatic events and as the mean interval time of the focal disturbance event with equal or greater magnitude for rare or occasional events. (b) Severity estimation was based on the effect size, which was calculated by comparing the population growth rate between the year when the disturbance event occurred and under normal conditions. Severity was represented by the return period, which was estimated as the inverse of the occurrence probability of the effect size.

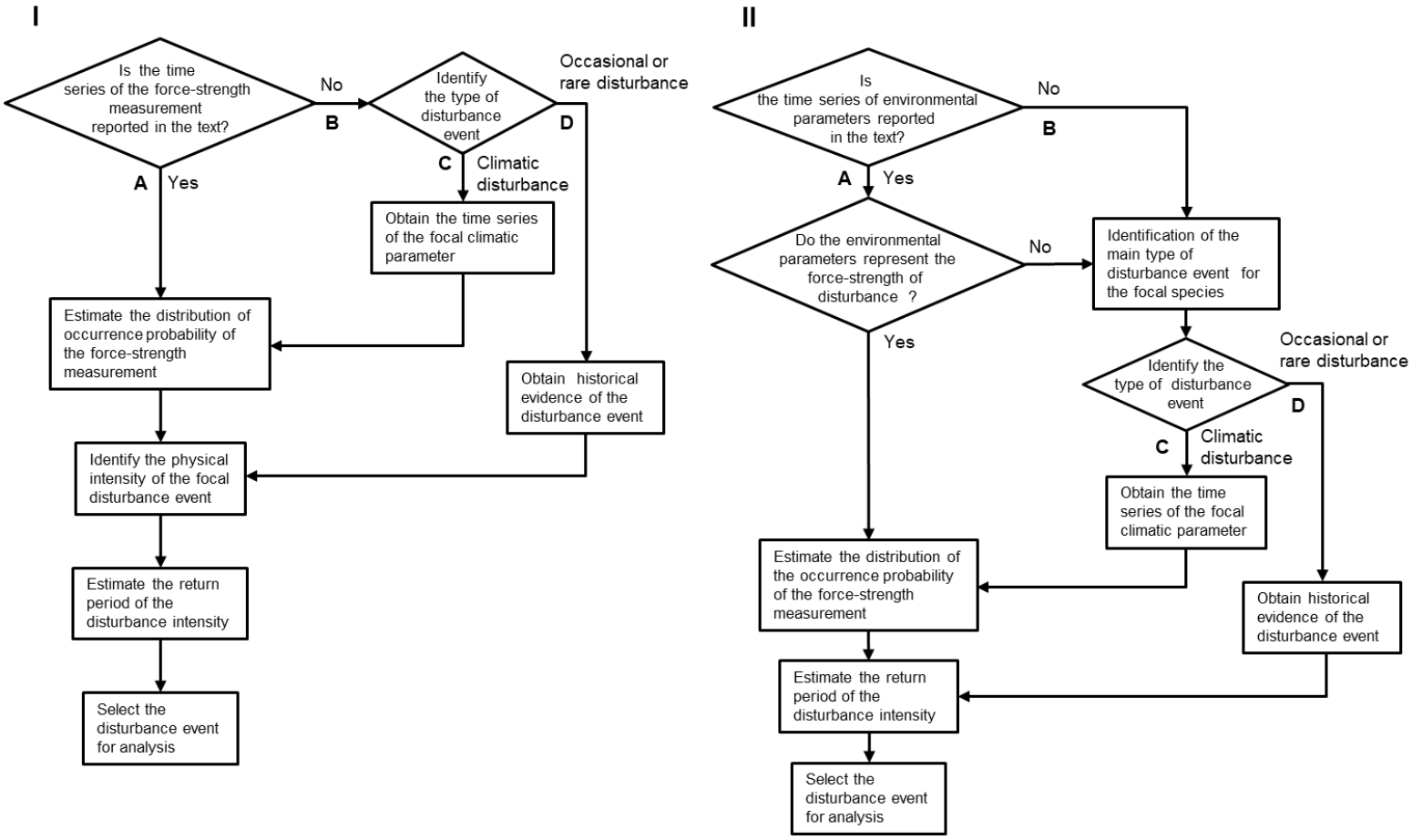


Figure A3-2. Flow chart of the estimation of intensity of a disturbance event. Two procedures used to estimate the intensity of the disturbance event that seemed to decrease the focal species abundance and occurred in the period of the study, for each time series: (I) when the disturbance event was reported in the original literature and (II) when no disturbance event was reported.

Table A3-1. Data used for the meta-analysis

Information about the disturbance events and species affected by those events. NOAA: U.S. National Oceanic and Atmospheric Administration; JMA: Japan Meteorological Association; GPDD: Global Population Dynamics Database (ver. 2); GS: Google Scholar; RPRI: authors' research project on a in rocky intertidal shore.

	Disturbance Event								Severity										
No.	Event No.	Year	Type of event	Force-strength measurement	Distribution of force-strength measurement	Length of record (years)	Return period of intensity (log_{10} years)	Data source	Record region	Species	Taxon (Class)	Habitat	Species trait	Normal period (years)	ES_i	95% CI of ES_i (lower, upper)	Return period (log_{10} years)	Time series source	Reference	Notes
1	1	1946	Severe winter	Winter minimum temperature	Extreme	107	1.76	Met Office	Central England	*Ardea cinerea*	Aves	Forest	Mobile	11	3.47	(2.13, 5.04)	3.58	GPDD	Lack (1954)	
2	2	1947	Severe winter	Maximum snow depth	Extreme	72	1.34	NOAA	Malcolm, Nebraska, US Bennet, Nebraska, US Raymond 2 E, Nebraska, US Lincoln University Power Plant, Nebraska, US	*Colinus virginianus*	Aves	Water system	Mobile	40	1.15	(0.84, 1.45)	0.90	GPDD	Nebraska Game and Parks Commission (1990)	
3	3	1983	Severe winter	Maximum snow depth	Extreme	72	1.92	NOAA	Malcolm, Nebraska, US Bennet, Nebraska, US Raymond 2 E, Nebraska, US Lincoln University Power Plant, Nebraska, US	*Colinus virginianus*	Aves	Water system	Mobile	40	1.26	(0.94, 1.57)	0.98	GPDD	Nebraska Game and Parks Commission (1990)	
4	4	1959	Severe winter	Maximum snow depth	Extreme	72	1.87	NOAA	Malcolm, Nebraska, US Bennet, Nebraska, US Raymond 2 E, Nebraska, US Lincoln University Power Plant, Nebraska, US	*Colinus virginianus*	Aves	Water system	Mobile	40	2.74	(2.26, 3.28)	2.51	GPDD	Nebraska Game and Parks Commission (1990)	
5	5	1951	Severe winter	Number of snow (>5 cm) days	Extreme	57	1.36	The original paper		*Tyto alba*	Aves	Forest	Mobile	31	0.35	(-0.11, 0.88)	0.44	GS	Altwegg et al. (2006)	
6	6	1952	Severe winter	Number of snow (>5 cm) days	Extreme	57	1.72	The original paper		*Tyto alba*	Aves	Forest	Mobile	31	2.71	(1.46, 4.28)	2.47	GS	Altwegg et al. (2006)	
7	7	1986	Severe winter	Number of snow (>5 cm) days	Extreme	57	1.32	The original paper		*Tyto alba*	Aves	Forest	Mobile	31	0.63	(0.08, 1.28)	0.58	GS	Altwegg et al. (2006)	
8	8	1976	Severe winter	Number of snow (>5 cm) days	Extreme	57	1.32	The original paper		*Tyto alba*	Aves	Forest	Mobile	31	0.80	(0.19, 1.50)	0.67	GS	Altwegg et al. (2006)	
9	9	1962	Severe winter	Number of snow (>5 cm) days	Extreme	57	2.00	The original paper		*Tyto alba*	Aves	Forest	Mobile	31	3.33	(1.86, 5.22)	3.36	GS	Altwegg et al. (2006)	
10	10	1956	Low temperature	Annual mean temperature	Normal	137	2.02	NOAA	Bamberg Germany	*Bupalus piniaria*	Insecta	Forest	Mobile	13	1.99	(1.42, 2.80)	1.63	GPDD	Klimetzek (1988)	Bavaria
11	10	1956	Low temperature	Annual mean temperature	Normal	137	2.02	NOAA	Bamberg, Germany	*Diprion pini*	Insecta	Forest	Mobile	16	0.04	(-0.58, 0.56)	0.32	GPDD	Klimetzek (1988)	Bavaria
12	10	1956	Low temperature	Annual mean temperature	Normal	137	2.02	NOAA	Bamberg, Germany	*Panolis flammea*	Insecta	Forest	Mobile	16	3.49	(2.08, 5.52)	3.62	GPDD	Klimetzek (1988)	Bavaria
13	11	1986	Low temperature	Average water temperature	Normal	106	1.30	The original paper		*Semibalanus balanoides*	Crustacea	Intertidal shore	Sessile	31	1.45	(0.94, 2.08)	1.13	GS	Hawkins et al. (2003)	
14	12	1962	Low temperature	Average temperature in Mar-May	Normal	106	1.66	Met Office	United Kingdom	*Parus major*	Aves	Forest	Mobile	15	0.21	(-0.35, 0.68)	0.38	GPDD	O'Connor (1980)	
15	13	1962	Severe winter	Mean temperature of winter (Dec-Mar)	Normal	105	2.57	NOAA	United Kingdom	*Alectoris rufa*	Aves	Farm land	Mobile	12	0.23	(-0.47, 0.72)	0.39	GPDD	Batten & Marchant (1977)	
16	13	1962	Severe winter	Mean temperature of winter (Dec-Mar)	Normal	105	2.57	NOAA	United Kingdom	*Perdix perdix*	Aves	Farm land	Mobile	12	0.93	(0.35, 1.51)	0.75	GPDD	Batten & Marchant (1977)	
17	13	1962	Severe winter	Mean temperature of winter (Dec-Mar)	Normal	105	2.57	NOAA	United Kingdom	*Vanellus vanellus*	Aves	Farm land	Mobile	8	5.82	(3.53, 11.13)	8.53	GPDD	Batten & Marchant (1977)	
18	13	1962	Severe winter	Mean temperature of winter (Dec-Mar)	Normal	105	2.57	NOAA	United Kingdom	*Gallinula chloropus*	Aves	Farm land	Mobile	11	10.53	(7.32, 15.35)	25.50	GPDD	Batten & Marchant (1977)	
19	13	1962	Severe winter	Mean temperature of winter (Dec-Mar)	Normal	105	2.57	NOAA	United Kingdom	*Carduelis carduelis*	Aves	Farm land	Mobile	11	0.75	(0.08, 1.52)	0.64	GPDD	Batten & Marchant (1977)	
20	13	1962	Severe winter	Mean temperature of winter (Dec-Mar)	Normal	105	2.57	NOAA	United Kingdom	*Motacilla alba*	Aves	Farm land	Mobile	10	7.29	(4.62, 11.27)	12.81	GPDD	Batten & Marchant (1977)	
21	14	1965	Severe winter	Mean temperature of winter (Dec-Mar)	Normal	50	1.82	NOAA	Alajarvi Moksy 1, Finland	*Sorex araneus*	Mammalia	Forest	Mobile	9	0.81	(-0.02, 1.64)	0.68	GPDD	Henttonen et al. (1989)	Eastern Finland
22	15	1968	Severe winter	Annual maximum snow accumulation	Extreme	28	1.76	The original paper		*Alces alces*	Mammalia	Forest	Mobile	24	1.89	(1.39, 2.52)	1.53	GS	Messier (1991)	
23	16	1969	Severe winter	Total snow precipitation	Normal	18	1.28	The original paper		*Aythya americana*	Aves	Wetland	Mobile	16	0.43	(-0.22, 0.94)	0.48	GPDD	Higgins et al. (1992)	
24	16	1969	Severe winter	Total snow precipitation	Normal	18	1.28	The original paper		*Oxyuya jamaicensis*	Aves	Wetland	Mobile	16	2.35	(1.64, 3.24)	2.03	GPDD	Higgins et al. (1992)	
25	17	1979	Severe winter	Total snow precipitation	Normal	18	1.40	The original paper		*Anas discors*	Aves	Wetland	Mobile	16	1.10	(0.38, 1.85)	0.87	GPDD	Higgins et al. (1992)	
26	17	1979	Severe winter	Total snow precipitation	Normal	18	1.40	The original paper		*Anas clypeata*	Aves	Wetland	Mobile	16	0.77	(0.26, 1.38)	0.66	GPDD	Higgins et al. (1992)	
27	17	1979	Severe winter	Total snow precipitation	Normal	18	1.40	The original paper		*Aythya americana*	Aves	Wetland	Mobile	16	0.33	(-0.30, 0.83)	0.43	GPDD	Higgins et al. (1992)	
28	17	1979	Severe winter	Total snow precipitation	Normal	18	1.40	The original paper		*Oxyuya jamaicensis*	Aves	Wetland	Mobile	16	0.65	(0.09, 1.20)	0.59	GPDD	Higgins et al. (1992)	
29	18	1971	Severe winter	Mean temperature of winter (Dec-Mar)	Normal	70	1.79	NOAA	Haines Junction, California, US	*Ovis dalli dalli*	Mammalia	Boreal forest and shrub	Mobile	10	0.57	(-0.07, 1.30)	0.55	GPDD	Hoefs & Bayer (1983)	
30	19	1984	Low temperature	Average temperature in spring	Normal	68	2.05	The original paper		*Lygacus equestris*	Insecta	Grassland	Mobile	7	0.81	(0.02, 2.35)	0.68	GS	Solbreck (1991)	
31	20	1987	Low temperature	Average temperature in spring	Normal	68	2.31	The original paper		*Lygacus equestris*	Insecta	Grassland	Mobile	7	8.56	(6.63, 13.58)	17.25	GS	Solbreck (1991)	
32	21	1989	Drought	Annual precipitation	Normal	119	1.52	The original paper		*Euura lasiolepis*	Insecta	Forest	Mobile	13	2.35	(1.71, 3.25)	2.03	GS	Hawkins & Holyoak (1998)	Arizona
33	22	1985	Drought	Annual precipitation	Normal	119	1.36	The original paper		*Coleophora laricella*	Insecta	Forest	Mobile	8	0.13	(-0.71, 0.81)	0.35	GS	Hawkins & Holyoak (1998)	Oregon
34	23	1985	Drought	Annual precipitation	Normal	19	1.64	The original paper		*Malacosoma pluviale*	Insecta	Forest	Mobile	10	0.03	(-0.69, 0.82)	0.31	GS	Hawkins & Holyoak (1998)	Victoria, BC
35	24	2006	Storm	Annual maximum wave height	Extreme	18	1.41	JMA	Tokachi, Japan	*Pterosiphonia bipinnata*	Phaeophyceae	Intertidal shore	Sessile	8	0.40	(-0.41, 1.10)	0.46	RPRI	Noda (unpublished data)	Doto
36	24	2006	Storm	Annual maximum wave height	Extreme	18	1.41	JMA	Tokachi, Japan	*Chthamalus challengeri*	Crustacea	Intertidal shore	Sessile	11	0.22	(-0.50, 0.83)	0.38	RPRI	Noda (unpublished data)	Doto
37	24	2006	Storm	Annual maximum wave height	Extreme	18	1.41	JMA	Tokachi, Japan	*Neosiphonia yendoi*	Chlorophyceae	Intertidal shore	Sessile	11	0.54	(-0.17, 1.64)	0.53	RPRI	Noda (unpublished data)	Doto
38	24	2006	Storm	Annual maximum wave height	Extreme	18	1.41	JMA	Tokachi, Japan	*Gloiopeltis furcata*	Florideophyceae	Intertidal shore	Sessile	11	0.85	(0.00, 1.78)	0.70	RPRI	Noda (unpublished data)	Doto
39	25	2006	Storm	Annual maximum wave height	Extreme	28	1.51	JMA	Kamaishi, Japan	*Chthamalus challengeri*	Crustacea	Intertidal shore	Sessile	6	0.31	(-0.69, 2.69)	0.42	RPRI	Noda (unpublished data)	Sanriku
40	25	2006	Storm	Annual maximum wave height	Extreme	28	1.51	JMA	Kamaishi, Japan	*Corallina pilulifera*	Florideophyceae	Intertidal shore	Sessile	6	0.05	(-2.50, 1.33)	0.32	RPRI	Noda (unpublished data)	Sanriku
41	25	2006	Storm	Annual maximum wave height	Extreme	28	1.51	JMA	Kamaishi, Japan	*Crassostrea gigas*	Bivalvia	Intertidal shore	Sessile	6	4.46	(3.06, 6.99)	5.39	RPRI	Noda (unpublished data)	Sanriku
42	25	2006	Storm	Annual maximum wave height	Extreme	28	1.51	JMA	Kamaishi, Japan	*Septifer virgatus*	Bivalvia	Intertidal shore	Sessile	5	3.40	(2.48, 6.32)	3.47	RPRI	Noda (unpublished data)	Sanriku
43	26	2006	Storm	Annual maximum wave height	Extreme	18	1.41	JMA	Tokachi, Japan	*Ralfsia verrucosa*	Phaeophyceae	Intertidal shore	Sessile	9	1.29	(0.40, 2.68)	1.01	RPRI	Noda (unpublished data)	Donan
44	26	2006	Storm	Annual maximum wave height	Extreme	18	1.41	JMA	Tokachi, Japan	*Leathesia marina*	Phaeophyceae	Intertidal shore	Sessile	10	0.73	(0.05, 1.57)	0.63	RPRI	Noda (unpublished data)	Donan
45	26	2006	Storm	Annual maximum wave height	Extreme	18	1.41	JMA	Tokachi, Japan	*Hildenbrandia rubra*	Florideophyceae	Intertidal shore	Sessile	10	1.01	(0.12, 1.78)	0.81	RPRI	Noda (unpublished data)	Donan
46	26	2006	Storm	Annual maximum wave height	Extreme	18	1.41	JMA	Tokachi, Japan	*Septifer virgatus*	Phaeophyceae	Intertidal shore	Sessile	10	1.09	(0.39, 1.79)	0.86	RPRI	Noda (unpublished data)	Donan
47	27	2011	Tsunami	Tsunami deposit	-	4000	2.46	Ishimura & Miyauchi (2015) [23]		*Chthamalus challengeri*	Crustacea	Intertidal shore	Sessile	6	0.51	(-0.50, 2.76)	0.52	RPRI	Noda (unpublished data)	
48	27	2011	Tsunami	Tsunami deposit	-	4000	2.46	Ishimura & Miyauchi (2015) [23]		*Corallina pilulifera*	Florideophyceae	Intertidal shore	Sessile	6	1.00	(0.41, 1.53)	0.80	RPRI	Noda (unpublished data)	
49	27	2011	Tsunami	Tsunami deposit	-	4000	2.46	Ishimura & Miyauchi (2015) [23]		*Crassostrea gigas*	Bivalvia	Intertidal shore	Sessile	6	1.83	(1.10, 2.90)	1.47	RPRI	Noda (unpublished data)	
50	27	2011	Tsunami	Tsunami deposit	-	4000	2.46	Ishimura & Miyauchi (2015) [23]		*Septifer virgatus*	Bivalvia	Intertidal shore	Sessile	5	3.40	(2.48, 6.32)	3.47	RPRI	Noda (unpublished data)	

Table A3-2. Reference used in the meta-analysis References used in the meta-analysis. A full listing of the 14 published literature and electronic sources used in the meta-analysis of the severity of disturbance events.

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12. O'Connor, R. J. (1980). Pattern and process in Great Tit (Parus major) populations in Britain. *Ardea*, 68(1-4), 165–183.
13. Solbreck, C. (1991). Unusual weather and insect population dynamics: Lygaeus equestris during an extinction and recovery period. *Oikos*, 60(3), 343–350.
14. Stafford, J. (1971). The heron population of England and Wales, 1928–1970. *Bird Study*, 18(4), 218–221.

Table A3-3. Selection criteria of time series of abundance for use in analysis.

Process	Category	Criteria of time series of abundance		Reason
		Type	Description	
i) Quality of time series of abundance	Purpose of study	Exclusion	Obtained for purposes other than estimation of wild population size	To exclude the effects of anthropogenic influence(s) such as fishing and hunting on abundance
	Resolution of abundance	Exclusion	Combined abundances of several species	To evaluate species-level severity
	Measure of abundance	Exclusion	Represented by relative abundance and indirect measurement	To ensure accuracy of the population dynamics of focal species
	Temporal trend	Exclusion	Representing significant (P<0.05) temporal trend in abundance by linear regression	To eliminate data on populations influenced by chronic stress other than the focal disturbance event during the whole recording period
	Spatial scale of study	Inclusion	Obtained by census conducted at a scale ≥10 km^2	To accurately estimate the general picture of the event's severity at a sufficient spatial scale relative to the scale of the event [1] [2]
	Length of time series	Exclusion	Length less than twice the generation time	To ensure accuracy of the population dynamics of the focal species and severity estimation by using sufficient length of time series relative to generation time of focal species [3]
ii) Target species	Seasonal migration	Exclusion	Observing migratory species	Difficulty in specifying the place and timing of population decline and the factor(s) causing it
	Generation time	Exclusion	Observing species with generation times <1 year	To avoid underestimation of severity caused by growth and reproduction occurring immediately after the disturbance
	Generation time	Exclusion	Observing species with generation times >10 years	To target the species that seem to experience the focal disturbance event less than once in two generations
iii) Requirement for calculation of severity	Abundance measured before and after disturbance event	Inclusion	Containing two abundance measures in the 1-year periods immediately before and after the disturbance	To estimate the population growth rate when the disturbance event occurred
	Abundance measured under normal conditions	Inclusion	Containing four annual abundance transitions under normal conditions	To ensure the estimation accuracy of the variability of population growth rate under normal conditions

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[1] Foster, D. R. (1988). Disturbance history, community organization and vegetation dynamics of the old-growth Pisgah Forest, south-western New Hampshire, USA. *Journal of Ecology*, 76(1), 105–134.

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Table A3-4. Values of Akaike's information criterion (AIC) and Schwarz Bayesian Information Criterion (BIC) for the regression models. The error distributions, link functions, the AIC values and the BIC values for the potential models of the generalized linear model.

Error distribution	Link function	AIC	BIC
Gamma	Log	161.76	167.50
Gamma	Inverse	163.27	169.00
Gaussian	Identity	287.36	293.10

Chapter IV

General discussion

This study provided both a measure of severity of disturbance impact which can be compared across species, and a measure of intensity of disturbance which can be compared across disturbance types. By using these, I demonstrated a quantitative evaluation of the severity of the 2011 Tohoku earthquake tsunami on rocky intertidal communities as a case study. In chapter 2, I evaluated the severity of impact of the tsunami on the rocky inter tidal communities on a regional scale. I found that the tsunami had a significant negative impact on the whole community and on one subgroup, mobiles, but not on the sessiles subgroup. In chapter 3, I quantified the severity–intensity relationship across disturbance types and species by using a meta-analysis. I found that the severity and the range of its 95% confidential interval increased exponentially with increasing intensity. In addition, I found the severity of the 2011 Tohoku earthquake tsunami was relatively small for rocky intertidal benthic organisms, despite the high intensity of the disturbance. In this chapter, I synthesized results of previous chapters and provided future prospects for researches on disturbance ecology. Especially, I focused on two topics: variation in severity of disturbance impact and applicability of the framework for quantifying severity-intensity relationship of disturbances.

4.1. Species traits associated with species vulnerability

The tsunami did not have a significant negative impact when evaluated as the degree of decline in population growth rate on sessiles, but it did on mobiles (in chapter 2). This interspecific difference in vulnerability to disturbance should depend on species traits (e.g., Sousa 2001; Mouilot *et al.* 2013), which fall into two categories. One is phenotypic

traits such as body size, and morphological and physiological properties. Among these traits, which trait plays an important role in determining species vulnerability should be largely dependent upon the kind of disturbance events, species phylogeny, and habitat types (e.g., Sousa 2001). For example, body size and morphological properties are major determinants of the capacity to resist water drag force for benthos (e.g., Denny et al. 1985). On the other hand, physiological properties, such as metabolic rate and temperature tolerance, determine capacity to resist physiological stress associated with abnormal weather for terrestrial organisms (e.g., Jiguet *et al.* 2006; Harrison *et al.* 2010). The other category of species traits, which strongly influenced species' vulnerability to disturbance, was life history traits such as generation time, dispersal ability, and fecundity (e.g., Zimmemian *et al.* 1994; Poorter *et al*. 2008) in the disturbance impact which is evaluated based on population growth rate. The role of each trait should be relatively consistent across the kinds of disturbances. For example, high dispersal ability or high fecundity decrease the impact of disturbance, because it allows a sufficient amount of immigration or recruitment which compensates mortality caused by disturbance (e.g., Pausas *et al.* 2004). Long generation time decreases the impact of rare but intense disturbance events, because a higher frequency of disturbance relative to the life span of an organism must exert stronger selection on the species to evolve disturbance resistance (Harper 1977).

Life history traits affect not only the species vulnerability to disturbance but also the speed of population recovery after disturbance. For example, high dispersal ability and high fecundity allow fast population recovery (e.g., Leibold *et al.* 2004; Bohrer *et al.* 2005; Pedley & Dolman 2014). On the other hand, long generation time, which involves small intrinsic growth rate, results in slow population recovery (Purvis *et al.* 2000; Huchings *et al.* 2012). In this study, to unify the return period of intensity for detecting the disturbance event, I limited the variation in generation time of species that were included in the dataset for analysis (chapter 3). However, it is a future challenge to analyze the data set with a wide range of variation in life history traits such as generation time, in the framework I proposed in chapter 3. Such analysis will greatly contribute to our understanding of ecological consequence of disturbances by evaluating how the intensity–severity relationship is influenced by event types and species life history traits.

4.2. Applicability of the framework for quantifying severity–intensity relationship of disturbances

In this study, I performed a meta-analysis to examine the severity–intensity relationship by focusing on the severity of a large-scale (≥10 km^2) disturbance event that had an extreme intensity value (Zscheischler *et al.* 2013), and occurred ≤5% of the time (≥20-year return period). The hypothetical species experienced such events no more than once in two generations (generation time ≤10 years). The framework I propose has broad applicability. First, it can be applied at various spatial or temporal scales and for species with various generation times. For example, the disturbance severity can be estimated for more frequent disturbances (e.g., heavy rain) or species with shorter generation times (e.g., microorganisms) at smaller spatial scales by using time series of abundance and physical measures of disturbance recorded at a shorter interval.

Second, it can be used to assess the impacts of disturbances on properties at the community level (e.g., species diversity) and ecosystem level (e.g., productivity), as well as at the population level (e.g., population growth rate in this study). In these cases, I can estimate the impact of a disturbance on the focal response property by using time series data on the response property and estimating the return period of the magnitude of change in the value caused by disturbance. Note, however, that the estimated impact at the community and ecosystem levels includes the indirect influence of disturbance.

Third, anthropogenic disturbances are also very important and are usually mixed with natural disturbances affecting ecosystems. Nevertheless, it is difficult to quantify the intensity of some anthropogenic disturbances, such as land-use change, pollution, and fishing and harvesting, because such disturbances act irreversibly (e.g., land use), slowly (e.g., pollution), or chronically (e.g., fishing and harvesting), so that our framework for quantifying the severity–intensity relationship is not directly applicable to these disturbances. However, the framework can be used to assess the interactive effect of anthropogenic disturbances and natural disturbances by comparing the severities of natural disturbances between habitats that are affected and not affected by anthropogenic disturbances.

Fourth, the severities of most intentional anthropogenic disturbances, such as

logging and use of pesticides, can be relatively readily quantified. By considering their severities in the severity–intensity relationship obtained from natural disturbances, it's possible to calculate the intensities of such anthropogenic disturbances by assuming that the severities are comparable to those caused by natural disturbances; such calculations may contribute to the risk management of intentional anthropogenic disturbances.

4.3. Conclusion

In this chapter, I discuss two topics: the effect of species traits on the vulnerability to disturbance and the applicability of a framework for quantifying the severity-intensity relationship. In the first topic, I conclude that the life history traits affect the severity of disturbance impact and recovery rate after disturbance. In the second topic, I conclude that the framework I propose would allow us to predict the ecological consequences of various kinds of disturbance events at multiple ecological levels (e.g., population, community, and ecosystem). Unfortunately, however, the current lack of long term census data makes these analyses, especially at the community and ecosystem-levels, impossible, highlighting that it's imperative that we start conducting long-term censuses of various kinds of organisms in different habitats.

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