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Effects of ocean current fluctuations on community dynamics in rocky intertidal habitat
（海流系変動が岩礁潮間帯ハビタットにおける群集動態に及ぼす効果）

Thesis
In partial fulfillment of the requirements
for the degree of Doctor of Environmental Science

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Chapter 1

1. I reviewed previous studies that examined community dynamics. The result showed that the quantification of community dynamics has been conducted using a variety of aggregate properties (community abundance, species richness, and diversity), univariate non-aggregate properties (individual species abundances), and multivariate non-aggregate properties (species composition), and that there are three main significances of the study of community dynamics: (1) to deepen our understanding of the variability of ecosystem, community, and population dynamics and its driving mechanisms, and (2) to deepen our understanding of many key ecological phenomena such as stability, succession, community assembly and synchrony, and (3) to elucidate the driving mechanisms of community dynamics.

2. I reviewed the studies on marine community dynamics. The results indicated that many previous studies analyze community dynamics after disturbance caused by experimental manipulation, while marine community dynamics after natural disturbance, in particular ocean current fluctuations, eruption, marine heatwave, ice scour, and freshwater flooding, have not been rarely examined yet. Future work should use long-term continuous community data, including periods before and after natural disturbances, to determine the effects of natural disturbances on community dynamics. Especially, influence of ocean current fluctuations on marine community dynamics is the most important topic of the research area. This is because ocean current fluctuations occur over a wide area and have a large spatial range of influence.

3. The target system was examined for assessing the effect of the ocean current fluctuations on community dynamics, and it was shown that the rocky intertidal

community is one of the best model systems.

Chapter 2

1. Evaluating the ecological resilience of communities is crucial for predicting their potential to recover from various natural disturbances such as ocean current fluctuations. In contrast, community temporal invariability can be relatively easily estimated for various metrics through short-term investigations. Thus, if ecological resilience can be estimated based on community temporal invariability, this would be advantageous from a management and conservation perspective.

2. I investigated spatial variation in patterns of a long-term trajectory of community dynamics representing different aspects of four ecological resilience (stable, reversible, abrupt, or linear) and temporal variability of species richness, species composition, and community abundance, as well as their interdependence by analyzing 16-year census data from 141 rocky intertidal sessile assemblages from six regions along the Pacific coast of Japan.

3. The result shows that while the stable trajectory was the most common, there was considerable difference in trajectory of community dynamics among regions, with a faster recovery to steady-state equilibrium in low-latitude regions. Furthermore, trajectories and various metrices of temporal variabilities varied among regions, depending on the strength of ocean current fluctuations. Thus, the relationship between community temporal invariability and trajectory may be weak or absent, at least at the regional scale.

4. In regions where fluctuations in the flow patterns of the ocean current are greater, temporal variability in species richness and species composition is greater, while temporal variability in community abundance is smaller. Temporal variability of species composition was greater near the Kuroshio Current than near the Oyashio, while temporal variability of community abundance was the opposite.

Chapter 3

1. Ocean current fluctuations are associated with the occurrence of marine heatwaves (MHWs), which are anomalously sea water temperature warm event, have increased. In recent years, the frequency and duration of MHWs. Therefore, there is an urgent need to understand the response of marine organisms to MHWs. However, there are several issues that have not yet been considered.

2. I investigated the response of rocky intertidal communities in the southeast Hokkaido to marine heat waves during 2010–2016 caused by ocean current fluctuations. I evaluated the impacts of MHWs on the abundances and species niche (thermal and vertical) traits of rocky intertidal communities (macroalgae, sessile invertebrates, herbivorous mollusks and carnivorous invertebrates) by separating the effect of environmental stochasticity.

3. I found that the accumulative carryover effects (i.e., continued increase or decrease in abundance with the number of years elapsed since the onset of the MHWs) of MHWs were detected both in the community abundance of functional groups and in the abundance of each species. Furthermore, the community abundance of macroalgae and herbivorous mollusk increased and decreased during MHWs and up to two years later, respectively. Thus, during and after MHWs, abundances of species with low thermal niches decreased and those with high thermal niches increased. The increase in abundance in warmer-water species due to MHWs is more pronounced for species with higher vertical niches, only when accumulative carryover effects were considered.

4. These results emphasize that the response of organisms to MHWs should be evaluated even when accumulative carryover effects are considered. There were few signs of community abundance recovery in the functional groups by the second year after the MHWs caused by ocean current fluctuations. Focusing on thermal niches can be useful for understanding and predicting the ecological processes of responses of marine

organisms to MHWs, while importance of vertical niches is still unknown.

Chapter 4

1. I summarized Chapter 1 to 3. Next, I discussed effects of ocean current fluctuations on community dynamics of marine organisms.

2. My study supported previous studies that spatiotemporal variations in ocean currents drive community dynamics. Therefore, the important role of ocean current fluctuations as a driver of marine community dynamics may be universal in marine ecosystems. However, since most of the evidences were obtained at the population level of single species or few species, assessments of the importance of ocean current fluctuations as a driver of marine community dynamics are awaited as future researches. My study also shows that analyses, using various properties, provides a comprehensive understanding of the impact of ocean current fluctuations on the community dynamics and a greater understanding of the processes and mechanisms behind that impact. It is recommended to take an approach, where multiple properties are quantified at the same time when evaluating the effects of ocean current fluctuations on community dynamics. Furthermore, my study demonstrates that long-term data over a period of 10 years is extremely useful in assessing the effects of ocean current fluctuations on community dynamics. Despite the outstanding efficacy of long-term data over 10 years to assess the effects of ocean current fluctuations on community dynamics, many previous studies have been conducted over relatively short time series.

3. In elucidating the response of community dynamics to ocean current fluctuations, the knowledge lacking in previous studies, including this study, is how species traits other than thermal niche are related to species response to ocean current fluctuations. Therefore, future studies are needed to evaluate and predict the effects of ocean current fluctuations on community dynamics, taking into account various species traits, such as nutritional

(trophic) niches, dispersity, in addition to thermal niche.

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Chapter 1

General Introduction

1.1. Significance of the study of community dynamics

In general, biological communities change over time. This is because communities are exposed to different natural and anthropogenic environmental changes that can cause changes in their composition. In addition to environmental changes, demographic stochasticity, and dispersal can also drive temporal changes in biological communities. Large number of previous studies focusing on temporal changes in biological communities have been conducted in various taxonomic groups in terrestrial and aquatic environments (Cusson et al. 2015; Gotelli et al. 2017; Houlahan et al. 2018; Pires et al. 2018; Smale et al. 2019; Hillebrand and Kunze. 2020; Avolio et al. 2021) and much knowledge has been accumulated. However, compared to spatial variation in communities, not much is known about community dynamics. For example, there are books on spatial ecology (Cantrell et al. 2010) but not on temporal ecology (Ryo et al. 2019). In addition, 300 000 versus 10 000 Google search hits of the terms ‘spatial ecology’ and ‘temporal ecology’, respectively (Ryo et al. 2019). It is a general pattern that the number of species increases with increasing area — species-area relationship, and a similar idea that the number of species increases with increasing of time period of survey — species-temporal relationship. Despite this interest in community dynamics is common to studies of spatial variation in communities, the reason why there are fewer studies of temporal changes compared to spatial variation is that spatial variation in communities can be evaluated for its patterns and processes by a one-time study (snapshot type study), whereas community dynamics require repeated studies in the same community.

To evaluate community dynamics, researchers should repeat surveys of the same community, in which community dynamics are quantified as changes in the values of specific community properties: aggregative properties (community abundance and diversity) and/or non-aggregative properties (individual species abundances (univariate) and community composition (multivariate)) (Table 1-1). Quantify changes in aggregative properties over time are changes in community abundance (e.g., Joseph and Cusson. 2015; Pinedo et al. 2015; Xu et al. 2019; Antão et al. 2020; Weitzman et al. 2021), or diversity (e.g., Munari. 2011; Joseph and Cusson. 2015; Pinedo et al. 2015; Xu et al. 2019; Antão et al. 2020; Weitzman et al. 2021). Clarifying dynamics in abundance of functional groups, the units of ecosystem components, and their driving factors will lead to an understanding of the dynamics of the ecosystem. Ecosystems are composed of multiple functional groups (e.g., Watling and Steneck. 1982; Steneck and Dethier. 1994; Peterson et al. 1998) that have similar modes of interaction with other groups of organisms. The exchange of materials and energy between these functional groups is the function of an ecosystem. Therefore, the aggregate properties of community abundance as a unit can be used to understand the patterns of dynamics in the entire community/ecosystem units. Moreover, measuring dynamics in aggregate properties is useful for understanding the processes of dynamics in the entire community. For example, by focusing on dynamics in species richness, the degree of species turnover in the entire community can be determined.

Univariate non-aggregative properties are quantified in individual species abundances (e.g., Southward. 1991; Menge et al. 1997; Noda et al. 2016; Ohgaki et al. 2019), so it will deepen our understanding of population dynamics. Because population ecology (i.e., understanding population dynamics) has primarily studied the variable characteristics and drivers of population dynamics for a single species (sometimes a small group of interacting species) (e.g., Southward. 1991; Ohgaki et al. 2019). Thus, quantification by univariate non-aggregative properties leads to an understanding of the physiological and ecological processes behind species differences through increases and decreases in the species of interest.

The quantification of multivariate non-aggregative properties is mainly done by multivariate measures, based on pairwise resemblances (similarity, dissimilarity or distance) among survey units (Anderson et al. 2011; Legendre and Legendre. 2012; Legendre et al. 2013; Borcard et al. 2018). When multivariate measures are used, they include the (dis) similarity between consecutive times (e.g., Donohue et al. 2013; Mrowicki et al. 2016) or the (dis) similarity between the reference time and each subsequent time (e.g., Bagchi et al. 2017; Miner et al. 2021). All species interact directly and indirectly with many other species in the community through predation, prey and competition (e.g., Sanford. 1999; Poore et al. 2012; Pulsford et al. 2016; Hacker et al. 2019). Therefore, if we focus on only a few species, we will not be able to understand neither the patterns nor the processes of dynamics of all species. Thus, quantifying at the community composition unit provides insights that cannot be revealed by intraspecific density and environmental factors alone for the single species unit focus.

There are several important implications of focusing on the properties of aggregate, univariate and multivariate non-aggregate properties, to reveal the community dynamics. First, it is possible to answer different ecological questions. Second, by answering several different ecological questions simultaneously, it is possible to further deepen our understanding of the patterns of community dynamics and the processes behind them. Third, even in the case of insufficient data, it is possible to obtain some scientific understanding of the characteristics of the community dynamics by use one of the properties.

Community dynamics are closely related to many key ecological phenomena. Because they are quantified by assessing the community dynamics itself. These themes include stability (Pimm. 1991; Grimm. 1996; Donohue et al. 2016; Kéfi et al. 2019), succession describing the development and trajectory of communities and ecosystems over time (relatively long times) after a known disturbance (Odum. 1969; Farrell. 1991; Young et al. 2001; Prach et al. 2007; Prach and Walker. 2011; Pulsford et al. 2016; Chang and Turner. 2019), community assembly describing rules and mechanisms (often stochastic factors such as priority effects) that dictate local diversity patterns formed from a regional species pool regardless of disturbance history (Young et al. 2001; Fukami et al. 2015; Chang and HilleRisLambers. 2016) and synchrony (Loreau and De Mazancourt. 2008; Gross et al. 2014; Valdivia et al. 2021a).

Among the phenomena closely related to biological community dynamics, the community stability has received particular attention recent years. Stability is a multidimensional concept consisting of several components (Pimm. 1984; Grimm and Wissel. 1997; Kéfi et al. 2019). Stability components include (1) resistance, which is the degree to which a change in community following a disturbance (Pimm. 1984; Hillebrand et al. 2018; Pennekamp et al. 2018; Radchuk et al. 2019), (2) engineering resilience/recovery, which is the capacity of a community to return to its undisturbed state following a disturbance (Thrush et al. 2009; Hillebrand et al. 2018; Ingrisch and

Bahn. 2018; Radchuk et al. 2019), (3) (in) variability, which is the (inverse of) coefficient of variation of a (in) variable in community of variation (Pimm. 1984; Houlahan et al. 2018; Antão et al. 2020) and (4) persistence, which is often used as a measure of the susceptibility of systems to invasion by new species or the loss of native species (Pimm. 1984; Donohue et al. 2013; Mrowicki et al. 2016). Thus, components of stability include not only assesses biological community dynamics in response to disturbance, but also the be evaluated when focusing on community dynamics without considering disturbance. The stability component also includes functional stability as quantified by aggregate properties and compositional stability as measured by non-aggregate properties. Examples of stability, quantified by aggregative properties, includes (1) the temporal (in) variability of the species richness or abundance, which is evaluated as the (inverse of) coefficient of variation of the species richness or abundance over time (Pimm. 1984; Bulleri et al. 2012; Donohue et al. 2013; Mrowicki et al. 2016; Antão et al. 2020), (2) the functional resistance, which is measured as the log response ratio of the abundance in a disturbed community compared to a control community at the first sampling after disturbance treatment (Hillebrand et al. 2018; Radchuk et al. 2019; Hillebrand and Kunze. 2020; Polazzo and Rico. 2021; Valdivia et al. 2021a, b), (3) the functional recovery, which is measured as the log response ratio of the abundance in a disturbed community compared to a control community at the final sampling (Hillebrand et al. 2018; Radchuk et al. 2019; Hillebrand and Kunze. 2020; Polazzo and Rico. 2021; Valdivia et al. 2021a, b). Examples of stability, assessed by non-aggregative properties includes (1) compositional turnover with aspects of persistence, which measured by the average of the jaccard (dis) similarity of consecutive surveys (Pimm. 1984; Donohue et al. 2013; Mrowicki et al. 2016; Eagle et al. 2021), (2) the compositional resistance, which is measured as Bray-Curtis (dis) similarity of the community composition between treatment and control at the first sampling after disturbance treatment, (3) the compositional recovery, which is measured as Bray-Curtis (dis) similarity of the community composition between treatment and control at the final sampling (Hillebrand et al. 2018; Radchuk et al. 2019; Hillebrand and Kunze. 2020; Polazzo and Rico. 2021; Valdivia et al. 2021a, b). Functional stability and compositional stability have different aspects, and both would need to know more about how these metrics are interrelated. For example, despite functional stability is stable, compositional stability is unstable due to more rapid changes in species composition through asynchronous fluctuations or compensatory dynamics. In this case, the interpretation would be the exact opposite.

As of 1997, there were 163 definitions of stability (Grimm & Wissel. 1997), and this stability component has increased over the years (Kéfi et al. 2019), although the number of stability components used in studies focusing on the relationship between stability components is generally 2~6 (Donohue et al. 2013; Mrowicki et al. 2016; Hillebrand et al. 2018; Pennekamp et al. 2018; Radchuk et al. 2019; Hillebrand and Kunze. 2020; White et al. 2020; Eagle et al. 2021; Polazzo and Rico. 2021; Valdivia et al. 2021a, b). As mentioned earlier, quantifying only one component of stability could change the interpretation of stability, but many previous studies have analyzed only one component (Donohue et al. 2016; Kéfi et al. 2019). Therefore, studies describing the relationship between stability components have increased in recent years (Donohue et al. 2013; Hillebrand et al. 2018; Pennekamp et al. 2018; Radchuk et al. 2019; Hillebrand and Kunze. 2020; White et al. 2020; Eagle et al. 2021; Polazzo and Rico. 2021; Valdivia et al. 2021a).

Thus, while the theme of research on community dynamics is aimed at a deeper understanding of various key ecological phenomena, another important goal of research on community dynamics is to understand the driving factors of community dynamics. Particular attention has been paid to natural disturbances and inorganic environmental factors, such as temporal changes in temperature and nutrient concentrations, as drivers of communities (Buma. 2015; Joseph and Cusson. 2015; Côté et al. 2016; Micheli et al. 2016; Cimon and Cusson. 2018; Iwasaki and Noda. 2018; Komatsu et al. 2019; Orr et al. 2020; Avolio et al. 2021).

1.2. Previous studies on marine community dynamics: a review

The number of publications of previous studies on marine community dynamics has been increasing in recent years. The number of studies of temporal changes in marine communities per year was less than 50 from 1990-2000, less than 105 from 2001-2010, and less than 190 from 2011-2021 (Fig. 1-1). From 1990 to 2021, the number of research on the marine community dynamics and that on ecology increased 59-fold and 10-fold, respectively (Fig. 1-2). While community dynamics have been quantified by using three types of properties, including aggregative properties, univariate non-aggregate properties, and multivariate non-aggregative properties (Table 1), the properties used to quantify marine community dynamics were biased; relatively, few studies quantify community dynamics at multivariate non-aggregative properties (Fig. 1-3).

Among the key ecological phenomena quantified by assessing the community dynamics themselves, i.e., stability, succession, community assembly, and synchrony, stability and succession were the key ecological phenomena that were most frequently studied in marine community dynamics (Fig. 1-4). Many previous studies dealing with stability aimed to deepen understanding of the factors affecting stability (Bulleri et al. 2012;

Mrowicki et al. 2016; Miner et al. 2021; Valdivia et al. 2021b) and tried to elucidated relationship among various properties of multiple stability components (Donohue et al. 2013; White et al. 2020; Valdivia et al. 2021a). Many previous studies dealing with succession aimed to clarify the temporal transitional patterns in various community properties and their underlying mechanism (Sousa. 1979; Lubchenco. 1983; Turner. 1983; Sousa. 1984; Farrell. 1991; McCook and Chapman. 1997; Foster et al. 2003; Petraitis and Dudgeon. 2005; Petraitis et al. 2009; Valdivia et al. 2014; Martins et al. 2018). A common trend in previous studies on marine community dynamics dealing with stability or succession is that many of them analyze community dynamics after disturbance caused by experimental manipulation (Sousa. 1979; Lubichenco. 1983; Turner. 1983; Sousa. 1984; Farrell. 1991; Foster et al. 2003; Petraitis and Dudgeon. 2005; Petraitis et al. 2009; Donohue et al. 2013; Valdivia et al. 2014; Mrowicki et al. 2016; Martins et al. 2018; White et al. 2020; Valdivia et al. 2021a, b), while marine community dynamics after natural disturbance have not been rarely examined yet. This may be because long-term community data, including periods before and after natural disturbances, have seldom been available from marine communities.

An important goal of research on community dynamics is to elucidate the driving factors of community dynamics. As drivers of community dynamics, disturbances and change in abiotic environmental factors have been particularly paid attention (Joseph and Cusson. 2015; Côté et al. 2016; Micheli. et al. 2016; Cimon and Cusson. 2018; Iwasaki and Noda. 2018; Orr et al. 2020). While in marine ecosystems, many environmental variables, such as temperature, nutrient, salinity, primary productivity, wave action, desiccation, and tidal action, have been considered to be the main causes of spatiotemporal variation in the abundance and distribution of marine organisms; Sanford et al. 1999; Menge et al. 2003; Nielsen and Navarrete. 2004; Schoch et al.

2006; Gomes and José. 2009; Vinueza et al. 2014; Kunze et al. 2021), these environmental factors: temperature, nutrient, salinity and primary productivity have been paid attention as driver of marine community dynamics (Fig. 1-5). While in marine ecosystems, various disturbance agents, such as upwelling fluctuation, cyclone, ocean current fluctuation, eruption, marine heatwave, ice scour and freshwater flooding, often significantly impact the abundance and distribution of marine organisms (Haymon et al. 1993; Menge et al. 2003; Nielsen and Navarrete. 2004; Guillemot et al. 2007; Munari. 2011; Petraitis et al. 2015; Russell. 2015; Noda et al. 2016; Wolff et al. 2016; Ohgaki et al. 2019), only two disturbance events: upwelling fluctuation and cyclone, have been paid attention as driver of community dynamics (Fig. 1-6). Many of them analyze community dynamics after disturbance caused by experimental manipulation (Sousa. 1979; Lubichenco. 1983; Turner. 1983; Sousa. 1984; Farrell. 1991; Foster et al. 2003; Petraitis and Dudgeon. 2005; Petraitis et al. 2009; Donohue et al. 2013; Valdivia et al. 2014; Mrowicki et al. 2016; Martins et al. 2018; White et al. 2020; Valdivia et al. 2021a, b), while marine community dynamics after natural disturbance have not been rarely examined yet. This may be because long-term community data, including periods before and after natural disturbances, have seldom been available from marine communities.

In summary, while many previous studies analyze community dynamics after disturbance caused by experimental manipulation, our knowledge about the marine community dynamics caused by various natural disturbance events on marine community dynamics, especially ocean current fluctuations, eruption, marine heatwave, ice scour, and freshwater flooding, is still limited. Thus, future works to aim to elucidate the effects of these natural disturbances on community dynamics using long-term community data, including periods before and after natural disturbances are eagerly awaited. Especially, influence of ocean current fluctuations on marine community dynamics is the most important topic of the research area. This is because ocean current fluctuations occur over a wide area and have a large spatial range of influence. In addition, ocean current fluctuations are also associated with the occurrence of marine heatwaves (e.g., Miyama et al. 2021).

1.3. Rocky intertidal communities: a model system for assessing the effects of ocean current fluctuations on community dynamics

Rocky intertidal communities are one of the best study systems for examining the effects of ocean current fluctuation on community dynamics. First, because the lifespan of most rocky intertidal organisms ranges from several months to several years, ocean current fluctuation is likely to be reflected in the community dynamics. Second, rocky intertidal communities consist of a wide range of unbiased taxa with various life forms, including macroalgae, sessile animals (bivalves, crustaceans, and coelenterate), herbivorous invertebrates (sea urchins and gastropods), and carnivorous invertebrates (starfish and gastropods; Okuda et al. 2010; Iwasaki et al. 2016), which ensures generality in assessing the effects of ocean current fluctuations on marine benthic communities. Third, rocky intertidal organisms can be easily and precisely identified, and their abundance can be accurately and non-destructively quantified, thus allowing for continuous and accurate quantification of a variety of community properties (Tsujino et al. 2010; Kanamori et al. 2017). Fourth, previous studies of rocky intertidal communities have accumulated a wealth of knowledge about the environmental factors that drive community dynamics (Menge et al. 1997; Menge. 2000; Menge et al. 2003; Nielsen and Navarrete. 2004; Schoch et al. 2006; Vinueza et al. 2014; Menge et al. 2015), which can help interpret the response of community dynamics to in ocean current fluctuations.

In the following chapters, I will evaluate the effects of ocean current fluctuations on rocky intertidal community dynamics. In chapter 2, I examine spatial variation that captures the trajectories of the community quantified by aggregate properties and multivariate non-aggregate properties as stability. In chapter 3, I quantify community dynamics by using aggregate and univariate non-aggregate properties to examine the underlying mechanisms.

References

Anderson, M. J., T. O. Crist, J. M. Chase, M. Vellend, B. D. Inouye, A. L. Freestone, N. J. Sanders, H. V. Cornell, L. S. Comita, K. F. Davies, S. P. Harrison, N. J. B. Kraft, J. C. Stegen, and N. G. Swenson. 2011. Navigating the multiple meanings of β diversity: A roadmap for the practicing ecologist. Ecology Letters 14:19–28.

Antão, L. H., J. Pöyry, R. Leinonen, and T. Roslin. 2020. Contrasting latitudinal patterns in diversity and stability in a high-latitude species-rich moth community. Global Ecology and Biogeography 29:896–907.

Avolio, M. L., K. J. Komatsu, S. L. Collins, E. Grman, S. E. Koerner, A. T. Tredennick, K. R. Wilcox, S. Baer, E. H. Boughton, A. J. Britton, B. Foster, L. Gough, M. Hovenden, F. Isbell, A. Jentsch, D. S. Johnson, A. K. Knapp, J. Kreyling, J. A. Langley, C. Lortie, R. L. McCulley, J. R. McLaren, P. B. Reich, E. W. Seabloom, M. D. Smith, K. N. Suding, K. B. Suttle, and P. M. Tognetti. 2021. Determinants of community compositional change are equally affected by global change. Ecology Letters 24:1892–1904.

Bagchi, S., N. J. Singh, D. D. Briske, B. T. Bestelmeyer, M. P. McClaran, and K. Murthy. 2017. Quantifying long-term plant community dynamics with movement models: Implications for ecological resilience: Implications. Ecological Applications 27:1514–1528.

Borcard, D., F. Gillet, and P. Legendre. 2018. Numerical Ecology with R. Springer Nature,Cham.

Bulleri, F., L. Benedetti-Cecchi, M. Cusson, E. Maggi, F. Arenas, R. Aspden, I. Bertocci, T. P. Crowe, D. Davoult, B. K. Eriksson, S. Fraschetti, C. Golléty, J. N. Griffin, S. R. Jenkins, J. Kotta, P. Kraufvelin, M. Molis, I. S. Pinto, A. Terlizzi, N. Valdivia, and D. M. Paterson. 2012. Temporal stability of European rocky shore assemblages: Variation across a latitudinal gradient and the role of habitat-formers. Oikos 121:1801–1809.

Buma, B. 2015. Disturbance interactions: Characterization, prediction, and the potential for cascading effects. Ecosphere 6:1–15.

Cantrell, R.S., C. Cosner., and S. Ruan.. 2010. Spatial ecology. Chapman and Hall/CRC, New York.

Côté, I. M., E. S. Darling, and C. J. Brown. 2016. Interactions among ecosystem stressors and their importance in conservation. Proceedings of the Royal Society B: Biological Sciences 283: 20152592.

Chang, C. C., and B. L. Turner. 2019. Ecological succession in a changing world. Journal of Ecology 107:503–509.

Chang, C., and J. HilleRisLambers. 2016. Integrating succession and community assembly perspectives [version 1; referees: 2 approved]. F1000Research 5:1–10.

Cimon, S., and M. Cusson. 2018. Impact of multiple disturbances and stress on the temporal trajectories and resilience of benthic intertidal communities. Ecosphere 9: e02467.

Donohue, I., H. Hillebrand, J. M. Montoya, O. L. Petchey, S. L. Pimm, M. S. Fowler, K. Healy, A. L. Jackson, M. Lurgi, D. McClean, N. E. O’Connor, E. J. O’Gorman, and Q. Yang. 2016. Navigating the complexity of ecological stability. Ecology letters 19:1172–1185.

Donohue, I., O. L. Petchey, J. M. Montoya, A. L. Jackson, L. Mcnally, M. Viana, K. Healy, M. Lurgi, N. E. O'Connor, and M. C. Emmerson. 2013. On the dimensionality of ecological stability. Ecology Letters 16:421–429.

Eagle, L. J. B., A. M. Milner, M. J. Klaar, J. L. Carrivick, M. Wilkes, and L. E. Brown. 2021. Extreme flood disturbance effects on multiple dimensions of river invertebrate community stability. Journal of Animal Ecology 90:2135–2146.

Farrell, T. M. 1991. Models and mechanisms of succession: An example from a rocky intertidal community. Ecological Monographs 61:95–113.

Foster, M. S., E. W. Nigg, L. M. Kiguchi, D. D. Hardin, and J. S. Pearse. 2003. Temporal variation and succession in an algal-dominated high intertidal assemblage. Journal of Experimental Marine Biology and Ecology 289:15–39.

Fukami, T. 2015. Historical contingency in community assembly: integrating niches, species pools, and priority effects. Annual Review of Ecology, Evolution, and Aystematics 46:1–23.

Gomes, T.P. and J.S. Rosa Filho. 2009. Composition and spatio-temporal variability of meiofauna community on a sandy beach in the Amazon region (Ajuruteua, Pará, Brazil). Iheringia. Série Zoologia 99:210–216.

Grimm, V. 1996. A down-to-earth assessment of stability concepts in ecology: Dreams, demands, and the real problems. Senckenbergiana Maritima 27:215–226.

Grimm, V., and C. Wissel. 1997. Babel, or the ecological stability discussions: An inventory and analysis of terminology and a guide for avoiding confusion. Oecologia 109:323–334.

Gross, K., B. J. Cardinale, J. W. Fox, A. Gonzalez, M. Loreau, H. Wayne Polley, P. B. Reich, and J. van Ruijven. 2014. Species richness and the temporal stability of biomass production: A new analysis of recent biodiversity experiments. American Naturalist 183:1–12.

Guillemot, N., P., Chabanet, and O. Le Pape. 2010. Cyclone effects on coral reef habitats in New Caledonia (South Pacific). Coral Reefs 29:445–453.

Hacker, S. D., B. A. Menge, K. J. Nielsen, F. Chan, and T. C. Gouhier. 2019. Regional processes are stronger determinants of rocky intertidal community dynamics than local biotic interactions. Ecology 100:1–12.

Haymon, R.M., D.J. Fornari, K.L. Von Damm, M.D. Lilley, M.R. Perfit, J.M. Edmond, W.C. Shanks III, R.A.Lutz, J.M. Grebmeier, S. Carbotte, and D. Wright 1993. Volcanic eruption of the mid-ocean ridge along the East Pacific Rise crest at 9 45–52′ N: Direct submersible observations of seafloor phenomena associated with an eruption event in April, 1991. Earth and Planetary Science Letters 119:85–101.

Hillebrand, H., and C. Kunze. 2020. Meta-analysis on pulse disturbances reveals differences in functional and compositional recovery across ecosystems. Ecology Letters 23:575–585.

Hillebrand, H., S. Langenheder, K. Lebret, E. Lindström, Ö. Östman, and M. Striebel. 2018. Decomposing multiple dimensions of stability in global change experiments. Ecology Letters 21:21–30.

Houlahan, J. E., D. J. Currie, K. Cottenie, G. S. Cumming, C. S. Findlay, S. D. Fuhlendorf, P. Legendre, E. H. Muldavin, D. Noble, R. Russell, R. D. Stevens, T. J. Willis, and S. M. Wondzell. 2018. Negative relationships between species richness and temporal variability are common but weak in natural systems. Ecology 99:2592–2604.

Ingrisch, J. and M. Bahn . 2018. Towards a comparable quantification of resilience. Trends in Ecology and Evolution 33:251–259.

Iwasaki, A., K. Fukaya, and T. Noda. 2016. Quantitative evaluation of the impact of the

Great East Japan Earthquake and tsunami on the rocky intertidal community. In Ecological impacts of tsunamis on coastal ecosystems: lessons from the Great East Japan Earthquake, Ecological research monographs (eds. Urabe, J. and T. Nakashizuka). Springer, Tokyo, pp. 35–46.

Iwasaki, A., and T. Noda. 2018. A framework for quantifying the relationship between intensity and severity of impact of disturbance across types of events and species. Scientific Reports 8:1–7.

Joseph, L., and M. Cusson. 2015. Resistance of benthic intertidal communities to multiple disturbances and stresses. Marine Ecology Progress Series 534:49–64.

Kanamori, Y., K. Fukaya, and T. Noda. 2017. Seasonal changes in community structure along a vertical gradient: patterns and processes in rocky intertidal sessile assemblages. Population Ecology 59:301–313.

Kéfi, S., V. Domínguez-García, I. Donohue, C. Fontaine, E. Thébault, and V. Dakos. 2019. Advancing our understanding of ecological stability. Ecology Letters 22:1349–1356.

Komatsu, K. J., M. L. Avolio, N. P. Lemoine, F. Isbell, E. Grman, G. R. Houseman, S. E. Koerner, D. S. Johnson, K. R. Wilcox, J. M. Alatalo, J. P. Anderson, R. Aerts, S. G. Baer, A. H. Baldwin, J. Bates, C. Beierkuhnlein, R. T. Belote, J. Blair, J. M. G. Bloor, P. J. Bohlen, E. W. Bork, E. H. Boughton, W. D. Bowman, A. J. Britton, J. F. Cahill, E. Chaneton, N. R. Chiariello, J. Cheng, S. L. Collins, J. H. C. Cornelissen, G. Du, A. Eskelinen, J. Firn, B. Foster, L. Gough, K. Gross, L. M. Hallet, X. Han, H. Harmens, M. J. Hovenden, A. Jagerbrand, A. Jentsch, C. Kern, K. Klanderud, A. K. Knapp, J. Kreyling, W. Li, Y. Luo, R. L. McCulley, J. R. McLaren, J. P. Megonigal, J. W. Morgan, V. Onipchenko, S. C. Pennings, J. S. Prevéy, J. N. Price, P. B. Reich, C. H. Robinson, F. L. Russell, O. E. Sala, E. W. Seabloom, M. D. Smith, N. A. Soudzilovskaia, L. Souza, K. Suding, K. B. Suttle,

T. Svejcar, D. Tilmand, P. Tognetti, R. Turkington, S. White, Z. Xu, L. Yahdjian, Q. Yu, P. Zhang, and Y. Zhang. 2019. Global change effects on plant communities are magnified by time and the number of global change factors imposed. Proceedings of the National Academy of Sciences of the United States of America 116:17867–17873.

Kunze, C., M. Wölfelschneider, and L. Rölfer. 2021. Multiple Driver Impacts on Rocky Intertidal Systems: The Need for an Integrated Approach. Frontiers in Marine Science 8:1–13.

Legendre, P. and L. Legendre, . 2012. Numerical ecology. Elsevier, Amsterdam.

Legendre, P., and M. De Cáceres. 2013. Beta diversity as the variance of community data: Dissimilarity coefficients and partitioning. Ecology Letters 16:951–963.

Loreau, M., and C. De Mazancourt. 2008. Species synchrony and its drivers: Neutral and nonneutral community dynamics in fluctuating environments. American Naturalist 172: E48–E66.

Lubchenco, J. 1983. Littorina and Fucus: effects of herbivores, substratum heterogeneity, and plant escapes during succession. Ecology 64:1116–1123.

Martins, G. M., F. Arenas, F. Tuya, R. Ramírez, A. I. Neto, and S. R. Jenkins. 2018. Successional convergence in experimentally disturbed intertidal communities. Oecologia 186:507–516.

McCook, L. J., and A. R. O. Chapman. 1997. Patterns and variations in natural succession following massive ice- scour of a rocky intertidal seashore. Journal of Experimental Marine Biology and Ecology 214:121–147.

Menge, B. A., B. A. Daley, P. A. Wheeler, E. Dahlhoff, E. Sanford, and P. T. Strub. 1997. Benthic-pelagic links and rocky intertidal communities: Bottom-up effects on top-down control? Proceedings of the National Academy of Sciences of the United States of America 94:14530–14535.

Menge, B.A., Gouhier, T.C., Hacker, S.D., Chan, F. and Nielsen, K.J., 2015. Are meta-ecosystems organized hierarchically? A model and test in rocky intertidal habitats. Ecological Monographs, 85: 213-233.

Menge, B. A., J. Lubchenco, M. E. S. Bracken, F. Chan, M. M. Foley, T. L. Freidenburg, S. D. Gaines, G. Hudson, C. Krenz, H. Leslie, D. N. L. Menge, R. Russell, and M. S. Webster. 2003. Coastal oceanography sets the pace of rocky intertidal community dynamics. Proceedings of the National Academy of Sciences of the United States of America 100:12229–12234.

Micheli, F., K. W. Heiman, C. V. Kappel, R. G. Martone, S. A. Sethi, G. C. Osio, S. Fraschetti, A. O. Shelton, and J. M. Tanner. 2016. Combined impacts of natural and human disturbances on rocky shore communities. Ocean and Coastal Management 126:42–50.

Miner, C. M., J. L. Burnaford, K. Ammann, B. H. Becker, S. C. Fradkin, S. Ostermann-Kelm, J. R. Smith, S. G. Whitaker, and P. T. Raimondi. 2021. Latitudinal variation in long-term stability of North American rocky intertidal communities. Journal of Animal Ecology 90:2077–2093.

Miyama, T., S. Minobe, and H. Goto. 2021. Marine Heatwave of Sea Surface Temperature of the Oyashio Region in Summer in 2010–2016. Frontiers in Marine Science 7:1–13.

Mrowicki, R. J., N. E. O’Connor, and I. Donohue. 2016. Temporal variability of a single population can determine the vulnerability of communities to perturbations. Journal of Ecology 104:887–897.

Munari, C. 2011. Effects of the 2003 European heatwave on the benthic community of a severe transitional ecosystem (Comacchio Saltworks, Italy). Marine Pollution Bulletin 62:2761–2770.

Nielsen, K. J., and S. A. Navarrete. 2004. Mesoscale regulation comes from the bottom-up: Intertidal interactions between consumers and upwelling. Ecology Letters 7:31–41.

Noda, T., A. Iwasaki, and K. Fukaya. 2016. Recovery of rocky intertidal zonation: Two years after the 2011 Great East Japan Earthquake. Journal of the Marine Biological Association of the United Kingdom 96:1549–1555.

Odum, E.P. 1969. The Strategy of Ecosystem Development: An understanding of ecological succession provides a basis for resolving man's conflict with nature. Science 164: 262–270.

Ohgaki, S. I., T. Kato, N. Kobayashi, H. Tanase, N. H. Kumagai, S. Ishida, T. Nakano, Y. Wada, and Y. Yusa. 2019. Effects of temperature and red tides on sea urchin abundance and species richness over 45 years in southern Japan. Ecological Indicators 96:684–693.

Okuda, T., T. Noda, T. Yamamoto, M. Hori, and M. Nakaoka. 2010. Contribution of environmental and spatial processes to rocky intertidal metacommunity structure. Acta Oecologica 36:413–422.

Orr, J. A., R. D. Vinebrooke, M. C. Jackson, K. J. Kroeker, R. L. Kordas, C. Mantyka-Pringle, P. J. van den Brink, F. de Laender, R. Stoks, M. Holmstrup, C. D. Matthaei, W. A. Monk, M. R. Penk, S. Leuzinger, R. B. Schäfer, and J. J. Piggott. 2020. Towards a unified study of multiple stressors: Divisions and common goals across research disciplines. Proceedings of the Royal Society B: Biological Sciences 287: 20200421.

Pennekamp, F., M. Pontarp, A. Tabi, F. Altermatt, R. Alther, Y. Choffat, E. A. Fronhofer, P. Ganesanandamoorthy, A. Garnier, J. I. Griffiths, S. Greene, K. Horgan, T. M. Massie, E. Mächler, G. M. Palamara, M. Seymour, and O. L. Petchey. 2018. Biodiversity increases and decreases ecosystem stability. Nature 563:109–112.

Peterson, G., C. R. Allen, and C. S. Holling. 1998. Ecological resilience, biodiversity, and scale. Ecosystems 1:6–18.

Petraitis, P. S., and S. R. Dudgeon. 2005. Divergent succession and implications for alternative states on rocky intertidal shores. Journal of Experimental Marine Biology and Ecology 326:14–26.

Petraitis, P. S., E. T. Methratta, E. C. Rhile, N. A. Vidargas, and S. R. Dudgeon. 2009. Experimental confirmation of multiple community states in a marine ecosystem. Oecologia 161:139–148.

Petraitis, P.S. and S.R. Dudgeon. 2015. Variation in recruitment and the establishment of alternative community states. Ecology 96:3186–3196.

Pimm, S. L. 1984. The complexity and stability of ecosystems. Nature 315:635–636.

Pimm, S.L., 1991. The balance of nature?: ecological issues in the conservation of species and communities. University of Chicago press, Chicago.

Pinedo, S., R. Arévalo, and E. Ballesteros. 2015. Seasonal dynamics of upper sublittoral assemblages on Mediterranean rocky shores along a eutrophication gradient. Estuarine, Coastal and Shelf Science 161:93–101.

Pires, A. P. F., D. S. Srivastava, and V. F. Farjalla. 2018. Is Biodiversity Able to Buffer Ecosystems from Climate Change? What We Know and What We Don’t. BioScience 68:273–280.

Polazzo, F., and A. Rico. 2021. Effects of multiple stressors on the dimensionality of ecological stability. Ecology Letters 24:1594–1606.

Poore, A. G. B., A. H. Campbell, R. A. Coleman, G. J. Edgar, V. Jormalainen, P. L. Reynolds, E. E. Sotka, J. J. Stachowicz, R. B. Taylor, M. A. Vanderklift, and J. Emmett Duffy. 2012. Global patterns in the impact of marine herbivores on benthic primary producers. Ecology Letters 15:912–922.

Prach, K., J. Leps., and M. Rejmanek. 2007. Old field succession in central Europe:

local and regional patterns. In Old fields: dynamics and restoration of abandoned farmland (eds. Cramer, V. A. and R. J. Hobbs). Island Press.Washington DC, pp. 180–201.

Prach, K., and L. R. Walker. 2011. Four opportunities for studies of ecological succession. Trends in Ecology and Evolution 26:119–123.

Pulsford, S. A., D. B. Lindenmayer, and D. A. Driscoll. 2016. A succession of theories: Purging redundancy from disturbance theory. Biological Reviews 91:148–167.

Radchuk, V., F. De Laender, J. S. Cabral, I. Boulangeat, M. Crawford, F. Bohn, J. De Raedt, C. Scherer, J. C. Svenning, K. Thonicke, F. M. Schurr, V. Grimm, and S. Kramer-Schadt. 2019. The dimensionality of stability depends on disturbance type. Ecology Letters 22:674–684.

Russell, I.A. 2015. Spatio-temporal variability of five surface water quality parameters in the Swartvlei estuarine lake system, South Africa. African Journal of Aquatic Science 40: 119–131.

Ryo, M., C. A. Aguilar-Trigueros, L. Pinek, L. A. H. Muller, and M. C. Rillig. 2019. Basic Principles of Temporal Dynamics. Trends in Ecology and Evolution 34:723–733.

Sanford, E. 1999. Regulation of keystone predation by small changes in ocean temperature. Science 283:2095–2097.

Schoch, G. C., B. A. Menge, G. Allison, M. Kavanaugh, S. A. Thompson, and S. A. Wood. 2006. Fifteen degrees of separation: Latitudinal gradients of rocky intertidal biota along the California Current. Limnology and Oceanography 51:2564–2585.

Smale, D. A., T. Wernberg, E. C. J. Oliver, M. Thomsen, B. P. Harvey, S. C. Straub, M. T. Burrows, L. V. Alexander, J. A. Benthuysen, M. G. Donat, M. Feng, A. J. Hobday, N. J. Holbrook, S. E. Perkins-Kirkpatrick, H. A. Scannell, A. Sen Gupta, B. L. Payne, and P. J. Moore. 2019. Marine heatwaves threaten global biodiversity and the provision of ecosystem services. Nature Climate Change 9:306–312.

Sousa, W. P. 1979. Experimental Investigations of Disturbance and Ecological Succession in a Rocky Intertidal Algal Community. Ecological Monographs 49:227–254.

Sousa, W. P. 1984. Intertidal mosaics: patch size, propagule availability, and spatially variable patterns of succession. Ecology 65:1918–1935.

Southward, A. J. 1991. Forty years of changes in species composition and population density of barnacles on a rocky shore near plymouth. Journal of the Marine Biological Association of the United Kingdom 71:495–513.

Steneck, R. S., and M. N. Dethier. 1994. A functional group approach to the structure of algal-dominated communities. Oikos 69:476–498.

Thrush, S. F., J. E. Hewitt, P. K. Dayton, G. Coco, A. M. Lohrer, A. Norkko, J. Norkko, and M. Chiantore. 2009. Forecasting the limits of resilience: Integrating empirical research with theory. Proceedings of the Royal Society B: Biological Sciences 276:3209–3217.

Tsujino, M., M. Hori, T. Okuda, M. Nakaoka, T. Yamamoto, and T. Noda. 2010. Distance decay of community dynamics in rocky intertidal sessile assemblages evaluated by transition matrix models. Population Ecology 52:171–180.

Turner, T. 1983. Complexity of early and middle successional stages in a rocky intertidal surfgrass community. Oecologia 60:56–65.

Valdivia, N., M. A. Aguilera, and B. R. Broitman. 2021a. High Dimensionality of the Stability of a Marine Benthic Ecosystem. Frontiers in Marine Science 7:1–15.

Valdivia, N., C. Buschbaum, and M. Thiel. 2014. Succession in intertidal mussel bed assemblages on different shores: Species mobility matters. Marine Ecology Progress Series 497:131–142.

Valdivia, N., D. N. López, E. Fica-Rojas, A. M. Catalán, M. A. Aguilera, M. Araya, C.

Betancourtt, K. Burgos-Andrade, T. Carvajal-Baldeon, V. Escares, S. Gartenstein, M. Grossmann, B. Gutiérrez, J. Kotta, D. F. Morales-Torres, B. Riedemann-Saldivia, S. M. Rodríguez, C. Velasco-Charpentier, V. I. Villalobos, and B. R. Broitman. 2021b. Stability of rocky intertidal communities, in response to species removal, varies across spatial scales. Oikos 130:1385–1398.

Vinueza, L. R., B. A. Menge, D. Ruiz, and D. M. Palacios. 2014. Oceanographic and climatic variation drive top-down/bottom-up coupling in the Galápagos intertidal meta-ecosystem. Ecological Monographs 84:411–434.

Watling, and R. . Steneck. 1982. Feeding Capabilities and Limitation of Herbivorous Molluscs: A Functional Group Approach. Marine Biology 68:299–319.

Weitzman, B., B. Konar, K. Iken, H. Coletti, D. Monson, R. Suryan, T. Dean, D. Hondolero, and M. Lindeberg. 2021. Changes in Rocky Intertidal Community Structure During a Marine Heatwave in the Northern Gulf of Alaska. Frontiers in Marine Science 8: 556820.

Wolff, N.H., A. Wong, R. Vitolo, K. Stolberg, K. Anthony, and P.J. Mumby. 2016. Temporal clustering of tropical cyclones on the Great Barrier Reef and its ecological importance. Coral Reefs 35: 613–623.

White, L., N. E. O’Connor, Q. Yang, M. C. Emmerson, and I. Donohue. 2020. Individual species provide multifaceted contributions to the stability of ecosystems. Nature Ecology and Evolution 4:1594–1601.

Xu, Y., D. Wan, Z. Xiao, H. Wu, and M. Jiang. 2019. Spatio-temporal dynamics of seedling communities are determined by seed input and habitat filtering in a subtropical montane forest. Forest Ecology and Management 449:117475.

Young, T. P., J. M. Chase, and R. T. Huddleston. 2001. Community succession and assembly: Comparing, contrasting and combining paradigms in the context of ecological restoration. Ecological Restoration 19:5–18.

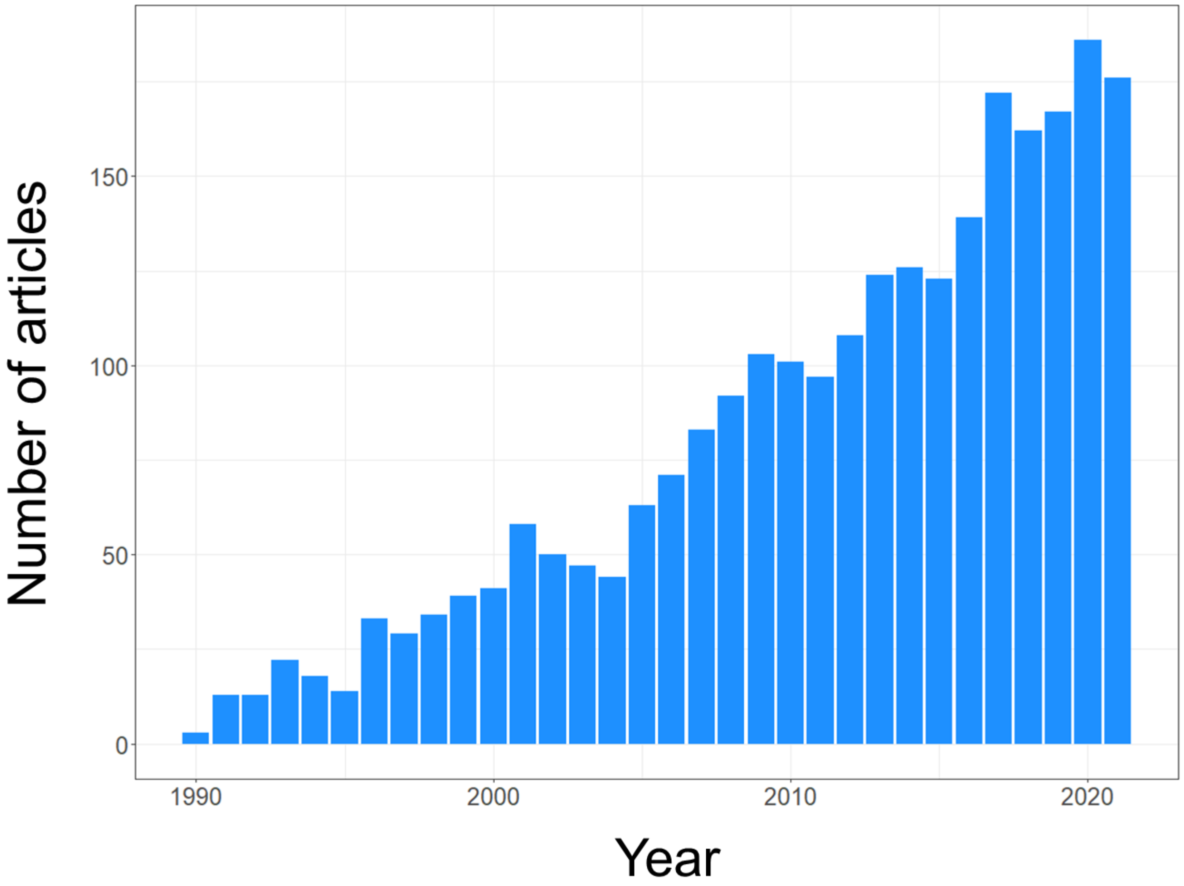


Fig. 1-1. Annual changes in the number of articles on marine community dynamics. I searched the Web of Science for articles published the period 1990–2021 using the following search statement: (“communit*” AND “trajector*” OR “communit*” AND “temporal change” OR “communit*” AND “temporal varia*” OR “community change” OR “community dynamic*”). Of these, I extracted marine communities by using the following search statement: (“rocky intertidal” OR “seaweed bed” OR “kelp bed” OR “sandy beach” OR “estuary” OR “coral reef” OR “mangrove” OR “deep sea” OR “hydrothermal” OR “cold seep” OR “pelagic”).

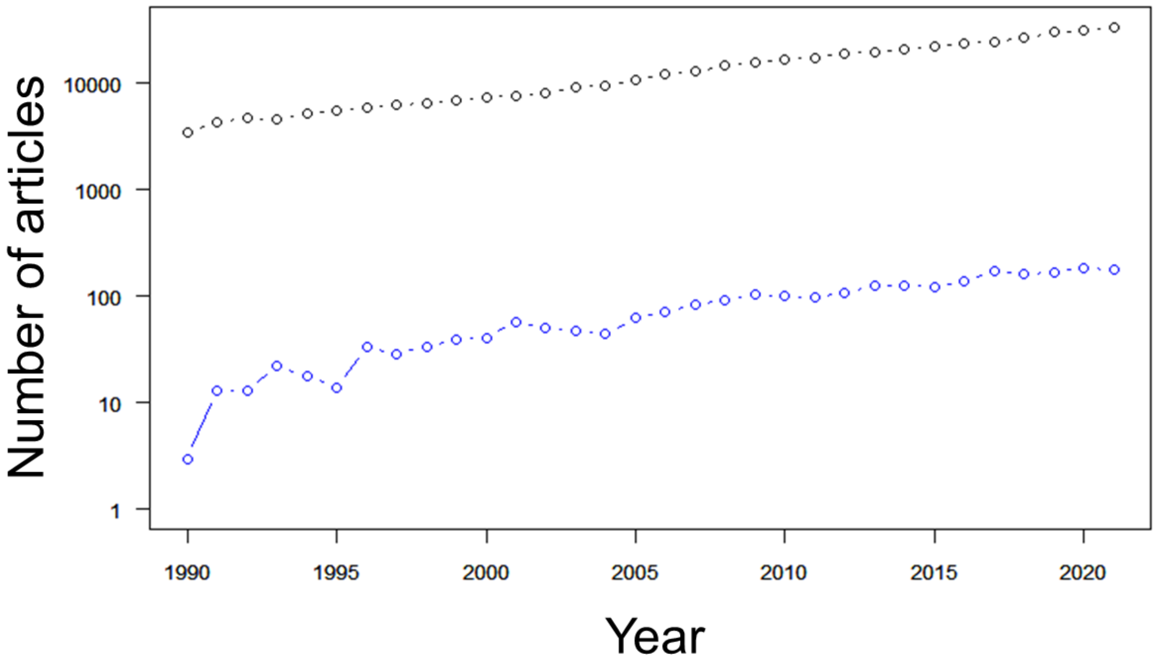


Fig. 1-2. Annual changes in the number of articles on marine community dynamics (blue; same data with Fig. 1-1), and in the number of previous studies on ecology (black: articles published the period 1990–2021 using the following search statement: (ecology) on Web of Science).

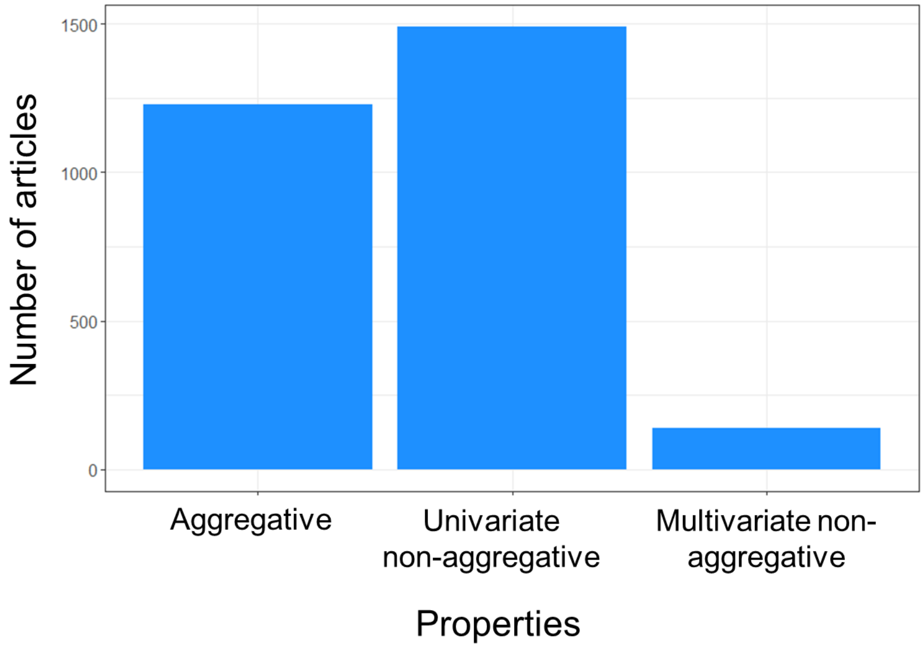


Fig. 1-3. Number of articles of marine community dynamics contain terms aggregative properties, univariate non-aggregate properties, and multivariate non-aggregative properties in the Web of Science for articles published the period 1990–2021 using the following search statement: (“community abundance” OR “community biomass” OR “community cover*” OR “community densit*” OR “total” AND “abundance” OR “total” AND “biomass” OR “total” AND “cover*” OR “total” AND “densit*” OR “species richness” OR “number of species” OR “diversity"), (“abundance” OR “biomass” OR “cover*” OR “densit*” NOT “community abundance” NOT “community biomass” NOT “community cover*” NOT “community densit*” NOT “total” AND “abundance” NOT “total” AND “biomass” NOT “total” AND “cover*” NOT “total” AND “densit*”), and (“similarit*” OR “dissimilarit*”) , respectively.

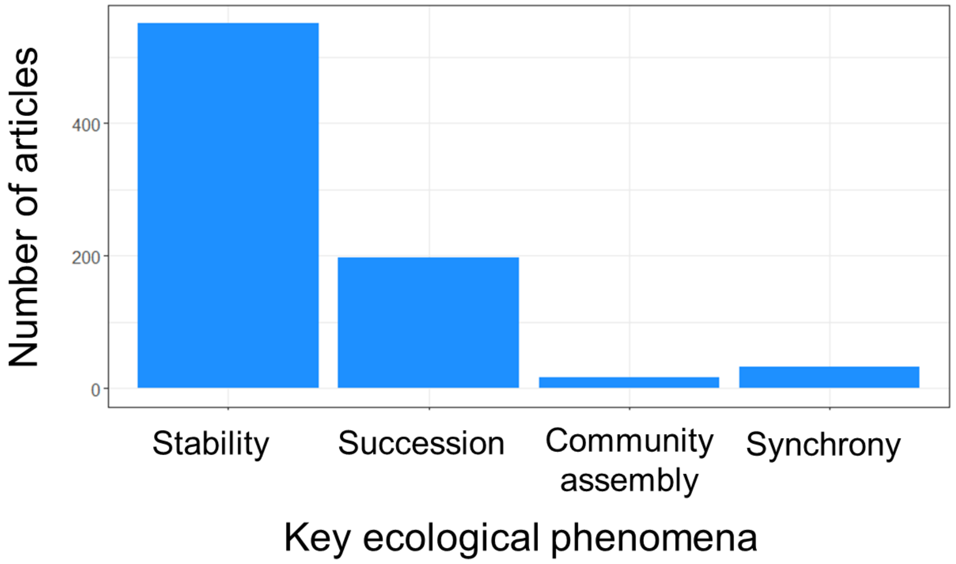


Fig. 1-4. Number of articles of marine community dynamics that contain terms stability, succession, community assembly, and synchrony in the Web of Science for articles published the period 1990–2021 using the following search statement: (“stability" OR "resilience" OR "resistance" OR "recovery" OR "persistence"), ("succession" OR "succession*"), ("community assembly"), and ("synchrony" OR "asynchrony" OR "synchronicity" OR "asynchronicity" OR "synchronous" OR "asynchronous"), respectively.

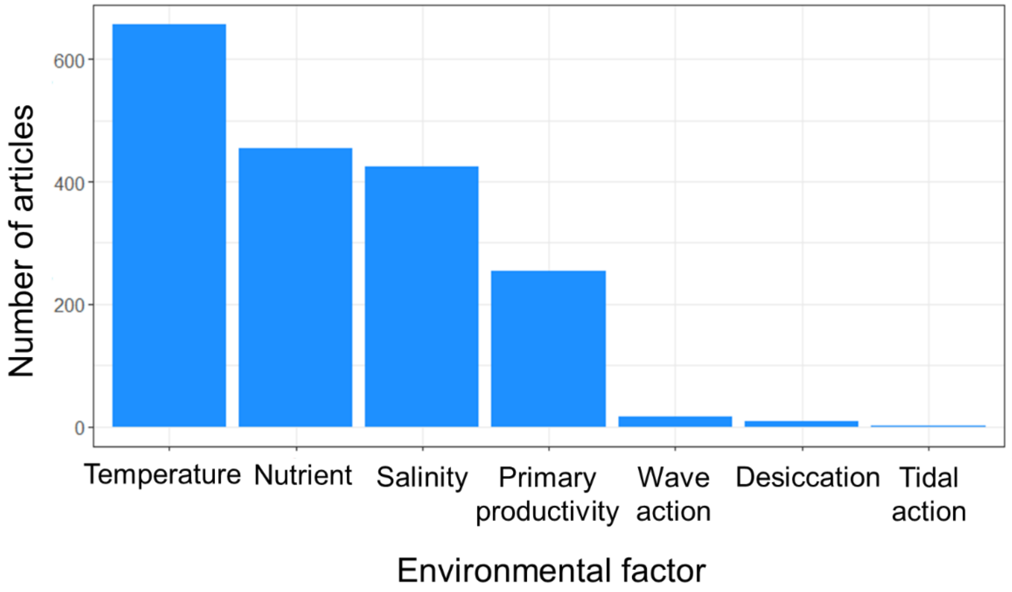


Fig. 1-5. Number of articles of marine community dynamics that contain terms temperature, nutrient, salinity, primary productivity, wave action, desiccation, and tidal action in the Web of Science for articles published the period 1990–2021 using the following search statement: (“"temperature" OR "temperature*"), ("nutrient*" OR "nutriments"), ("salinity"), ("chlorophyll a" OR "chlorophylla" OR "Chl a" OR "Chl-a" OR "chlorophyll-a"),("wave action" OR "wave-action") ,("desiccation" OR "aerial exposure"), and ("tidal action" OR "tidal-action" OR "tidal level fluctuat*"), respectively.

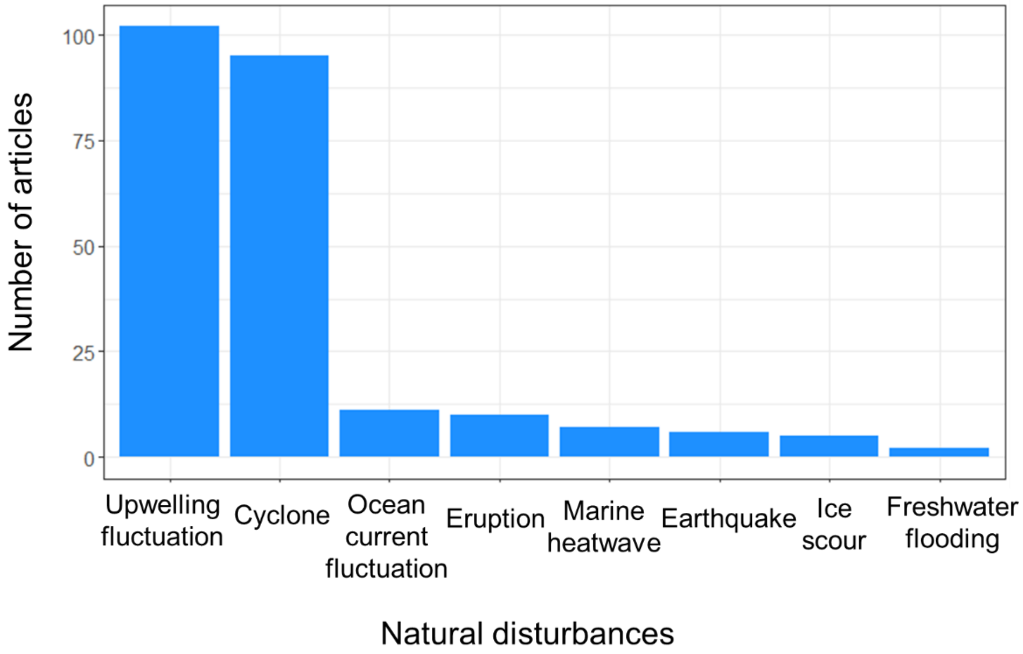
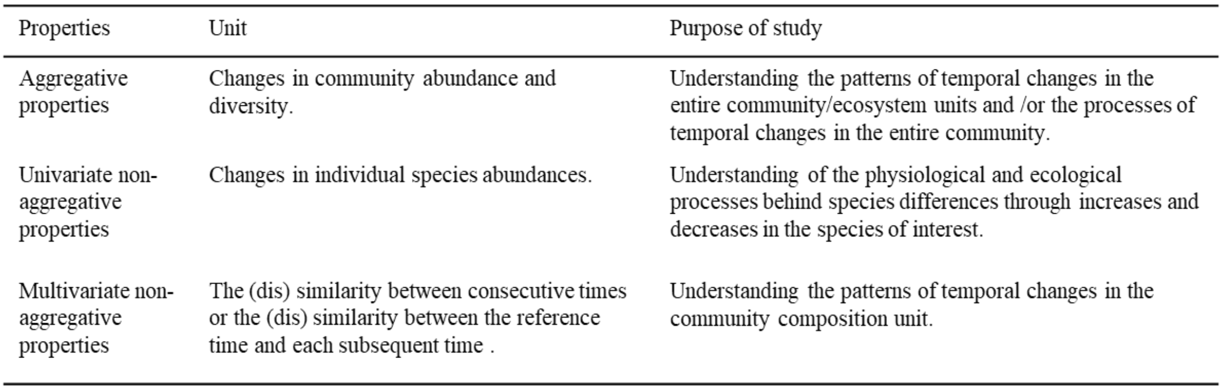


Fig. 1-6. Number of articles of marine community dynamics that contain terms upwelling fluctuation, cyclone, ocean current fluctuation, eruption, marine heat wave, earthquake, ice scour, and freshwater flooding in the Web of Science for articles published the period 1990–2021 using the following search statement: ("upwelling*" OR "upwelling fluctuation*"), ("cyclone" OR "cyclonic" OR "storm" OR "typhoon" OR "hurricane" OR "willy-willy" OR "tornado"), ("ocean current*" OR "ocean current fluctuation*"), ("eruption" OR "eructation" OR "lava flow" OR "volcanic ash"),("marine heatwave" OR "marine heatwaves") ,("earthquake" OR "earthquakes" OR "earth-quake" OR "earth-quakes"), ("ice scour" OR "ice-scour" OR "ice scour*" OR "ice-scour*" OR "drift ice" OR "ice drift"), and ("freshwater flooding") respectively.

Table 1-1. Properties and their Unit and Purpose of study to evaluate dynamics of biological communities.



Properties	Unit	Purpose of study
Aggregative properties	Changes in community abundance and diversity.	Understanding the patterns of temporal changes in the entire community/ecosystem units and /or the processes of temporal changes in the entire community.
Univariate non-aggregative properties	Changes in individual species abundances.	Understanding of the physiological and ecological processes behind species differences through increases and decreases in the species of interest.
Multivariate non-aggregative properties	The (dis) similarity between consecutive times or the (dis) similarity between the reference time and each subsequent time .	Understanding the patterns of temporal changes in the community composition unit.

Chapter 2

Quantifying the dynamics of rocky intertidal sessile communities along the Pacific coast of Japan: implications for ecological resilience

2.1. Introduction

The composition of biological communities generally varies temporally because of environmental changes and ephemeral disturbances, the magnitude and frequency of which vary with location. It is therefore crucial for the proper management and conservation of ecosystems to quantify patterns of community trajectories and to assess their spatial variability. Understanding patterns of community trajectories also provides insights into ecological resilience—that is, the movement of a community within and between stable domains (Holling et al. 1996; Peterson et al. 1998; Gunderson. 2000; Thrush et al. 2009)—which is useful for community conservation and for predicting the potential of a community to recover from various disturbances. Bagchi et al. (2017) developed an empirical method that allows researchers to categorize the dynamics of a focal community into one of four trajectories: stable (i.e., species composition does not undergo any appreciable change over time), abrupt (a relatively sudden change in community composition), reversible (the community undergoes major changes in composition and later returns to the original state), and linear (slow, incremental change in community composition over time) (Fig. 2-1, Table 2-1). The stable trajectory is defined by using an asymptotic model from the onset of movement away from a community defined as the baseline community as

$$(\mathrm{SDI})_t = \phi_1\,[1 - (\phi_2 t)], \tag{1}$$

where $(\mathrm{SDI})_t$ is the Sørensen dissimilarity index relative to the baseline community at time t, ϕ_1 is the asymptote at steady-state equilibrium, and ϕ_2 is the logarithm of the rate constant.

The abrupt trajectory is defined by a logistic model as

$$(\mathrm{SDI})_t = \frac{\delta}{1+exp(\frac{\theta-t}{\phi})}, \tag{2}$$

where δ is asymptotic height, θ is the time at which divergence (i.e., deviation from the baseline community) reaches half of δ, ϕ is the time between reaching one-half and three-quarters of the maximum divergence from the baseline community, and t is the time since the beginning of the record.

The reversible trajectory is defined by a double sigmoid mathematical function that estimates the distance, timing of onset and return phases (θ_o and θ_r, respectively), and duration of onset and return (ϕ_o and ϕ_r, respectively) as

$$(\mathrm{SDI})_t = \frac{\delta_o}{1+exp(\frac{\theta_o-t}{\phi_o})} - \frac{\delta_r}{1+exp(\frac{\theta_r-t}{\phi_r})}. \tag{3}$$

Here δ_o and δ_r are the asymptotic heights for onset and return phases of community change, θ_o and θ_r are the times of onset and return phases at which change reaches one-half of its asymptotic height, and ϕ_o and ϕ_r are the times elapsed between reaching one-half and three-quarters of the change distance for onset and return phases, respectively. t is the time interval from the beginning of the record.

Finally, the linear trajectory is defined with a linear model as

$$(\mathrm{SDI})_t = \alpha t + \varepsilon, \tag{4}$$

where α is the diffusion constant, t denotes the time since the beginning of the record, and ε is an error term representing the intercept. These four trajectories provide a quantitative basis to compare and interpret ecological resilience, because each trajectory is related to distinct concepts of ecological resilience. However, trajectory analysis requires a long-term census of the community.

In contrast, temporal invariability of a community can be relatively easily measured. For example, it doesn't require long-term census, many temporal replicates and fitting to mathematical models, and it has been quantified for both aggregative properties (e.g., community biomass) and non-aggregative properties (e.g., community composition) for various communities, depending on the research topic and question (Tilman et al. 2006; Hillebrand et al. 2018; Radchuk et al. 2019). In this study, I defined temporal invariability as the coefficient of variation (CV; aggregative properties) or mean (non-aggregative properties) of a variable over time (Donohue et al. 2013). Both ecological resilience and temporal invariability are components of community stability, which is a multidimensional concept (Pimm. 1984; Donohue et al. 2013; Donohue et al. 2016; Hillebrand et al. 2018; Pennekamp et al. 2018; Radchuk et al. 2019; Kéfi et al. 2019). The relationship between components of com-munity stability may depend on the properties by which the components of stability are measured (Hillebrand et al. 2018; Radchuk et al. 2019). Therefore, elucidating how community trajectories covary with temporal invariability, which has been quantified for various community properties, across space provides a good opportunity to deepen our understanding of the dimensionality of community stability. Also, it provides insights of efficient strategies for evaluating the community trajectories. For example, it is reasonable to predict that the temporal invariability for communities with a stable trajectory is higher than for those with other trajectories.

There are several fundamental questions related to the spatial variation of trajectories and temporal invariability of a biological community. First, do the prevalences of the four trajectories vary spatially? Second, do the features (model coefficients) of these trajectories vary spatially? The answers to these two questions will improve our understanding of the consistency and variability in both quantitative and qualitative features of the trajectories of natural biological communities. Third, how do temporal invariabilities change among different trajectories or regions? Addressing this question should provide knowledge useful for predicting the trajectories of natural communities, understanding multidimensionality of stability and the interdependencies between components.

Rocky intertidal sessile communities are some of the best study systems for examining spatial variation of trajectories and temporal invariability. First, intertidal rocky shores are common and accessible habitats and have a suite of usually well-described and easily identifiable species (Raffaelli and Hawkins.1996). Second, temporal changes in a rocky intertidal sessile community can be easily and non-destructively quantified as presence-or-absence and percent-coverage data at the same site because of the organisms' sessile growth habit. In addition, the community dynamics occurs at a tractable time scale because the component species of rocky intertidal communities have relatively short life spans. Previous studies demonstrated that the pace of community dynamics (Tsujino et al. 2010; Kanamori et al. 2017) and the strength of its determinant factors, such as larval flux, growth rate, and the strength of interspecific interactions, varied spatially depending on the coastal oceanography, such as intensity and frequency of upwelling (Menge et al. 1997; Sanford. 1999; Menge. 2000; Connolly et al. 2001; Menge et al. 2003; Nielsen et al. 2004; Schoch et al. 2006; Vinueza et al. 2014; Menge et al. 2015; Hacker et al. 2019).

Here, I examined how the community dynamics of rocky intertidal sessile assemblages on the steep slopes of rocks vary spatially along the Northwestern Pacific coast of Japan (between 31°N and 43°N) by explicitly incorporating hierarchical spatial scale into the monitoring design. I specifically investigated (1) how the relative prevalence of four trajectories differs among regions, (2) how the features of each trajectory vary among regions, and (3) how the temporal invariability of species richness, species composition, and community abundance differs among trajectories or regions, or both. Specifically, I hypothesized that regional differences in these trajectories and in the community invariability of rocky intertidal sessile community dynamics along the Pacific coast of Japan are governed by spatiotemporal variability of the ocean current systems. The study area is in the Kuroshio–Oyashio transition area, where the warm Kuroshio Current meets the cold Oyashio Current, and there are marked differences in abiotic environmental factors between these currents (Qiu. 2001; Qiu. 2002; Sakurai. 2007; Yatsu et al. 2013). The differences in environmental factors that reflect the current systems would likely cause differences in patterns of community dynamics.

Both the Kuroshio and Oyashio Currents show spatial and temporal fluctuations (Qiu. 2001; Qiu. 2002; Kawabe. 2005; Sakurai. 2007; Yatsu et al. 2013; Okunishi et al. 2018; Japan Meteorological Agency). Previous studies have suggested that spatiotemporal variability of these ocean current systems has likely caused changes in dominant species (Taniguchi et al.1986; Nomura, and Hirabayashi.2018), recruitment strength(Taniguchi et al.1986; Yamaguchi.1986; Ohgaki et al.2019), mortality (Kawajiri et al. 1981; Takami et al. 2008; Nomura, and Hirabayashi. 2018), and abundance of coastal organisms (Kawajiri et al. 1981; Taniguchi et al. 1986; Yamaguchi. 1986; Nomura, and Hirabayashi. 2018; Ohgaki et al. 2019). Therefore, I speculate that increasing spatiotemporal variability of ocean current systems increases the relative frequencies of the linear, reversible, and abrupt trajectories and some model coefficients of each trajectory (α of the linear, δ_o and δ_r of the reversible, ϕ_1 of the stable, and δ of the abrupt trajectory) and decreases the relative frequency of the stable trajectory and three measures of community temporal invariability: species richness, species composition, and community abundance.

2.2. Materials and methods

Census design

I used hierarchical nested sampling (Noda. 2004) for the layout of each site. Five rocky shores were chosen for the census of intertidal sessile organisms in each of six regions (eastern Hokkaido, southern Hokkaido, Rikuchu, Boso, Nanki, and Osumi; Fig. 2-2) along the Pacific coast of Japan between latitudes 31°N and 43°N, with intervals between neighboring regions of 263–513 km (mean ± SD: 404.9 ± 107.3 km; Sahara et al. 2015). Coastal marine biota in the area is affected by two major current systems: the warm Kuroshio along the southwestern coast and the cold Oyashio from the eastern coast of Hokkaido to the northeastern coast of Honshu (Fig. 2-2a; Qiu. 2001; Sakurai. 2007; Yatsu et al. 2013). The three northern regions are under the influence of the Oyashio Current, with conditional influence from the Tsugaru Warm Current, a branch of the Kuroshio, to southern Hokkaido and Rikuchu (Qiu. 2001; Hanawa and Mitsudera. 1987; Ohtani. 1987;

Takasugi. 1992; Takasugi and Yasuda. 1994). The Oyashio and the Tsugaru Warm Current show interannual variations; the southern limit of Oyashio intrusion changes as does the outflow pattern of the Tsugaru Warm Current (Conlon. 1982; Isoda and Suzuki. 2004; Sakurai. 2007; Okunishi et al. 2018). Among the three northern regions in my study, the southern limit of the first Oyashio intrusion—that is, the first branch of the Oyashio southward migration—is closest to Rikuchu and farthest from eastern Hokkaido (Okunishi et al. 2018). The three southern regions are strongly influenced by the Kuroshio. The Kuroshio also shows marked path fluctuations; the variability of the distance between the three southern regions and the main Kuroshio axis is smallest at Osumi, followed by Boso, with the greatest variability at Nanki (Qiu. 2001; Kawabe. 2005). In March 2011, the Rikuchu census area subsided 50 cm and experienced a tsunami, with local wave heights of 8–15 m, due to the Great East Japan Earthquake (Noda et al. 2016).

Within each region, I chose five shores at intervals of 2.7–17 km (8.2 ± 4.3 km; Sahara et al.2015) along the coastline (Fig. 2-2b). Within each shore, I established five 5000-cm^2 permanent census plots (the total number of plots was 150) on steep rock walls in semi-exposed locations at intervals of 3.1–378 m (37.3 ± 48.9 m; Sahara et al.2015). Each plot was 50 cm wide by 100 cm high, with the vertical midpoint corresponding to mean tidal level. The vertical extent of the permanent plots covered 72.4% of the tidal range (138.2 cm between mean high water and mean low water of spring tides; Noda et al. 2016). The angles of the rock walls in the plots varied between 41° and 103° (71.6° ± 15.8°; Sahara et al.2015) from horizontal (0°). Although the slopes varied across sites, most census sites (all plots except three) had slopes of 50°–100°, neither moderate nor overhanging. Detailed study-site descriptions and biogeographic features of the area are presented elsewhere (Okuda et al. 2004; Nakaoka et al. 2006). In each census plot, the presence or absence of all sessile species within a quadrat was recorded by eye, whereas coverage of sessile organisms was determined by counting their occurrence at 200 grid points at intervals of 5 cm both vertically and horizontally from 2003 to 2018. From 2007 on, I was unable to survey 9 out of 150 plots, for example those buried by sediments.

Data analysis

Community trajectory analysis. I quantified rates and patterns of community dynamics following methods described elsewhere (Bagchi et al. 2017). From presence/absence data for sessile organisms in individual census plots, I calculated the Sørensen dissimilarity index as a time series for successive years relative to the initial year. For both presence/absence and coverage data, I excluded rare taxa that accounted for < 2% of records in each region during the survey period. The frequency of occurrence of each taxon of sessile organism in each region is in Table S2-2. I next fitted the dissimilarity estimates from each census plot to mathematical functions defining each trajectory (i.e., I determined the model coefficients of each trajectory).

Finally, I judged the models' goodness-of-fit with the concordance criterion (CC), which measures the level of agreement between observed and predicted values for linear and nonlinear models. CC ≤ 0 indicates lack of fit, and CC = 1 indicates perfect fit, where

$$\mathrm{CC}_i = 1 - \frac{\sum_{j=1}^{n_i}\left(y_{ij}-\hat{y}_{ij}\right)^2}{\sum_{j=1}^{n_i}\left(y_{ij}-\bar{y}\right)^2+\sum_{j=1}^{n_i}\left(\hat{y}_{ij}-\bar{\hat{y}}\right)^2+n_i\left(\bar{y}-\bar{\hat{y}}\right)^2}. \qquad (5)$$

Here $\bar{y}$ and $\bar{\hat{y}}$ are the means of observed (y_{ij}) and predicted ($\bar{\hat{y}}_{ij}$) values for sample i, respectively, and n_i is the sample-specific number of observations in the time series.

I judged parsimony by using the Akaike information criterion (AIC); competing models with $\Delta\text{AIC} \leq 2$ were included as trajectories for a community. I first checked whether the fitted model yielded meaningful coefficient estimates. Here, I verified if the coefficients were of the correct sign and distinguishable from zero at $P = 0.10$ (e.g., whether $\alpha > 0$ for the fitted linear model). Second, I checked if the model with the highest CC was also supported by the AIC. If not, I checked the model with the second-highest CC and its corresponding AIC. If no winning model emerged at this third step, I then considered the plot "unresolved". This three-step screening to identify the best-fit model ensures that (1) a model is built with meaningful coefficients, (2) the coefficients well-describe the data, and (3) all coefficients are necessary. From the coefficients, CC, and AIC of each model, I classified the trajectory for each plot as stable, reversible, abrupt, or linear. Detailed descriptions of this method are available elsewhere (Bagchi et al. 2017).

Temporal community invariability

I estimated the temporal invariability of species richness, species composition, and community abundance for each plot. Temporal invariability of species richness was calculated as the inverse of the coefficient of variation (CV) of species richness from presence/absence data. Temporal invariability of species composition was the mean of the Jaccard similarity in sessile community composition (calculated from species presence/absence data) between consecutive years (Pimm. 1984; Mrowicki et al. 2016). Finally, temporal invariability of community abundance was calculated from coverage data as the inverse of the CV of total sessile community coverage (Bulleri et al. 2012; Donohue et al. 2016).

Statistical analysis

To detect regional differences in the proportional distribution of trajectories, I performed Fisher's exact test by using Monte Carlo simulations with 10,000 iterations. The following analyses were applied to local communities with linear or stable trajectories because my trajectory analyses showed that most correctly categorized trajectories were linear or stable (Fig. 2-3). To evaluate how community stability varied among regions within each trajectory, I performed one-way analysis of variance (ANOVA), in which each coefficient estimate of the best-fit model was treated as a response variable, and region was a fixed factor. To evaluate how temporal invariability of species richness, species composition, and community abundance varied among regions and trajectories, I performed two-way ANOVA, in which the response variables were (1) the inverse of the CV of species richness, (2) the mean of the Jaccard similarity between consecutive years, and (3) the inverse of the CV of total sessile community cover, as indicators of temporal invariability, and region and trajectory (linear or stable) were fixed factors. For significant ANOVAs ($P < 0.05$), I performed post hoc Bonferroni pairwise comparisons to evaluate differences between significant groups.

To examine how differences in current systems and the strength of current fluctuations influenced trajectories and temporal invariability of species richness, species composition, and community abundance, I performed multiple regression analyses, in which each trajectory coefficient and the three measures of temporal invariability were treated as response variables, and current systems and current fluctuations were explanatory variables. Here, current system was defined as a dummy variable (Kuroshio = 0, Oyashio = 1), and current fluctuations in each current system were assigned categorical values in descending order of fluctuation in the flow patterns of the ocean current (eastern Hokkaido = 1, southern Hokkaido = 2, Rikuchu = 3, Boso = 2, Nanki = 3, and Osumi = 1). All ANOVAs and multiple regressions were performed after checking the homogeneity of variance of the data (Levene's test) and applying the appropriate transformation. To evaluate the interdependence among the three measures of temporal community invariability, I calculated Spearman's rank correlation coefficients. All statistical analyses were executed with R version 3.5.2.

2.3. Results

The stable trajectory was the most common of the four trajectories, followed by the linear trajectory (except at Rikuchu and Osumi). The abrupt trajectory was detected only in eastern Hokkaido and at Rikuchu, and the reversible trajectory was not detected (Fig. 2-3). The proportions of trajectories differed significantly among regions (Fisher's exact test, $P < 0.001$).

All coefficients (α, a coefficient of the linear trajectory, and ϕ_1 and ϕ_2, coefficients of the stable trajectory) estimated from the best-fit models varied significantly among regions (Table S2-1). At the sites with linear dynamics, the Osumi community was more invariant than the Nanki community (parameter α; Table 2-2). At the sites with stable dynamics, community stability around the steady-state equilibrium in southern Hokkaido was higher than that of other regions (parameter ϕ_1) and the recovery rates to steady-state equilibrium in the Nanki and Osumi communities were faster than those of other regions (parameter ϕ_2; Table 2-2). Multiple regression analyses suggest that parameters α and ϕ_1 were higher with stronger current fluctuations, and parameter ϕ_2 was lower in areas under the influence of the Kuroshio Current (Table 2-3).

There was a significant interaction between region and trajectory for the temporal invariability of species richness. However, neither the temporal invariability of species composition nor community abundance varied significantly among trajectory types (Table 2-4).

The temporal invariability of species richness, species composition, and community abundance varied among regions (Table 2-4). The species richness of communities in Osumi classified as having linear trajectories was more invariable than that of communities in southern Hokkaido with linear trajectories and those in Nanki with stable trajectories (Fig. 2-4a). The species composition of communities in eastern Hokkaido and Osumi were significantly more stable than those in other regions (Fig. 2-4b). Community abundance at sites in southern Hokkaido and Boso was more stable than that in other regions (Fig. 2-4c).

Current fluctuation reduced the temporal invariability of both species richness and species composition while increasing the temporal invariability of community abundance (Table 2-3). Kuroshio Current regions exhibited lower temporal invariability of species composition but higher temporal invariability of community abundance than Oyashio Current regions (Table 2-3). Significant correlations were detected among the three measures of temporal invariability. The mean of the Jaccard similarity between consecutive years was positively correlated with the inverse of the CV of species richness, whereas it was negatively correlated with the inverse of the CV of community abundance (Fig. S2-1).

2.4. Discussion

The study area is located in the Kuroshio–Oyashio transition area, in which the Oyashio is characterized by low temperature, low salinity, and high primary productivity and the Kuroshio is characterized warmer temperatures, higher salinities, and generally low primary productivity (Qiu. 2001; Qiu. 2002; Sakurai. 2007; Yatsu et al. 2013). Previous studies in the area have shown that species richness in intertidal sessile assemblages within each region decreases with increasing latitude (Okuda et al. 2004), and a cluster analysis of similarities showed that the rocky intertidal assemblages could be first classified overall into two groups (comprising the three northern regions and the three southern regions), and then further separated into distinct groups for each region, except for the two southern regions (Nanki and Osumi; Nakaoka et al.2006). Despite these previously reported regional differences, I found a consistent pattern in the proportional distribution of trajectories across regions. The stable trajectory was the most common, followed by linear, whereas the other trajectories were rarely detected. A similar pattern has been observed in perennial grass communities, where stable and linear trajectories were the first and second most common, respectively (Bagchi et al. 2017). In plant and animal communities across the globe, the majority exhibit regulated fluctuations of both species richness and total abundance (Gotelli et al. 2017). In addition, both within and across meta-analyses that include terrestrial and aquatic systems, threshold transgressions are rarely detectable (Hillebrand et al. 2020). These studies suggest that biological communities are generally regulated. Furthermore, the trajectories in common between rocky intertidal sessile assemblages and perennial grass communities at the regional scale suggest that some sessile communities in marine benthic and terrestrial habitats show stable or linear dynamics. Testing this hypothesis will require more research on the spatial variation of trajectories in various habitats and taxa.

I did find a significant regional difference in the relative frequency of trajectories (Fisher's exact test; $P < 0.001$). Interestingly, the frequency of the stable trajectory per plot was the highest at Rikuchu, despite this site experiencing subsidence and a large tsunami during the 2011 Great East Japan Earthquake. This result suggests that the impact of the March 2011 earthquake on rocky intertidal sessile community dynamics was relatively small (Iwasaki. et al. 2016). Although the earthquake obviously affected the population size of some sessile species (Noda. et al. 2016, 2017), it did not significantly affect the dynamics of species composition in the local communities.

The linear trajectory is defined by using a linear model in which α is the diffusion constant; the stable trajectory is defined by using an asymptotic model in which ϕ_1 is the asymptote at steady-state equilibrium and ϕ_2 is the logarithm of the rate constant (Bagchi et al. 2017). α and ϕ_1 increased with greater current fluctuation. These results appear to support the idea that variation in environmental conditions influences species composition (Nuvoloni et al. 2016). ϕ_2 was lower for communities influenced by the Kuroshio Current (Nanki and Osumi in particular) than for those influenced by the Oyashio Current and in other regions. This suggests a faster recovery to steady-state equilibrium in regions at lower latitudes, presumably because marine organisms living in warmer environments are faster growing and shorter lived (Clarke. 1983; Moss et al. 2016).

I found that the relationship between community trajectories and temporal invariability was absent or weak. The trajectory analysis method that I used (Bagchi et al. 2017) provides an accurate and robust method for distinguishing community dynamics that provides insights into characteristics of ecological resilience and their interpretation; however, it requires long-term census data for the community, many temporal replicates and fitting to mathematical models. In contrast, community temporal invariability is easier to estimate. Therefore, if a community trajectory could be estimated from the community temporal invariability, it would not only advance our understanding of the multidimensional nature of community stability (Pimm. 1984; Donohue et al. 2013; Donohue et al. 2016; Kéfi et al. 2019) but would also greatly improve our ability to establish plans for the sustainable use and conservation of ecosystems by predicting natural community dynamics. Here, I examined whether there is a relationship between these trajectories and temporal invariability. My results did not show any clear relationship, at least for rocky intertidal sessile communities, indicating that direct estimation is necessary to identify the trajectories of a community. To clarify this issue, further research is necessary on the relationship between community temporal invariability and ecological resilience for rocky intertidal sessile communities and for other community types.

Temporal invariability of species richness, species composition, and community abundance are components of stability that characterize community dynamics. Therefore, understanding their spatial variation is crucial for the evaluation and management of ecosystems. Here, I detected significant differences between regions and between ocean current systems in the temporal invariability of species composition and community abundance of rocky intertidal sessile communities. The temporal invariability of biomass of an algal assemblage was shown to decrease with increasing latitude along the European coast (Bulleri et al. 2012). This pattern could result from a decrease in the mean value or an increase in the standard deviation of the aggregate property, or both (Bulleri et al. 2012). My results show that the temporal invariability of community abundance was less stable near the Oyashio Current (that is, at higher latitudes) than near the Kuroshio. However, it did not show an explicit trend along a latitudinal gradient. As expected, the effect of spatiotemporal fluctuations in the flow patterns of ocean currents emerged in the temporal invariability of species richness, species composition and community abundance of rocky intertidal sessile communities.

2.5. Conclusions

The present study examined how community dynamics of intertidal sessile assemblages on steep rocky slopes vary spatially along the Northwestern Pacific coast of Japan between 31°N and 43°N. The majority of communities exhibited stable dynamics in species composition (i.e., species composition did not undergo any appreciable change) during the 16 years studied. I found no clear interdependence between the community trajectories and quantified temporal invariabilities for species richness, species composition, or community abundance. Therefore, direct estimation is necessary to identify the trajectories of a community. Regional differences were detected in both trajectories and temporal invariabilities, associated with spatiotemporal variability of the ocean current systems in this area. Future research is needed to elucidate the linkage between spatiotemporal variability of the ocean current systems in the Kuroshio–Oyashio transition area and the dynamics of rocky intertidal sessile communities.

References

Bagchi, S., N. J. Singh, D. D. Briske, B. T. Bestelmeyer, M. P. McClaran, and K. Murthy. 2017. Quantifying long-term plant community dynamics with movement models: Implications for ecological resilience: Implications. Ecological Applications 27:1514–1528.

Bulleri, F., L. Benedetti-Cecchi, M. Cusson, E. Maggi, F. Arenas, R. Aspden, I. Bertocci, T. P. Crowe, D. Davoult, B. K. Eriksson, S. Fraschetti, C. Golléty, J. N. Griffin, S. R. Jenkins, J. Kotta, P. Kraufvelin, M. Molis, I. S. Pinto, A. Terlizzi, N. Valdivia, and D. M. Paterson. 2012. Temporal stability of European rocky shore assemblages: Variation across a latitudinal gradient and the role of habitat-formers. Oikos 121:1801–1809.

Clarke, A. 1983. Life in cold water: the physiological ecology of polar marine ectotherms. Oceanography and Marine biology 21:341–453.

Conlon, D.M. 1982. On the outflow modes of the Tsugaru Warm current. La mer 20: 60–64.

Connolly, S. R., B. A. Menge, and J. Roughgarden. 2001. A latitudinal gradient in recruitment of intertidal invertebrates in the northeast Pacific Ocean. Ecology 82:1799–1813.

Donohue, I., H. Hillebrand, J. M. Montoya, O. L. Petchey, S. L. Pimm, M. S. Fowler, K. Healy, A. L. Jackson, M. Lurgi, D. McClean, N. E. O'Connor, E. J. O'Gorman, and Q. Yang. 2016. Navigating the complexity of ecological stability. Ecology Letters 19:1172–1185.

Donohue, I., O. L. Petchey, J. M. Montoya, A. L. Jackson, L. Mcnally, M. Viana, K. Healy, M. Lurgi, N. E. O'Connor, and M. C. Emmerson. 2013. On the dimensionality of ecological stability. Ecology Letters 16:421–429.

Gotelli, N. J., H. Shimadzu, M. Dornelas, B. McGill, F. Moyes, and A. E. Magurran. 2017. Community-level regulation of temporal trends in biodiversity. Science Advances 3: e1700315.

Gunderson, L. H. Ecological resilience—in theory and application. 2000. Annual

Review of Ecology and Systematics 31:425–439.

Hacker, S. D., B. A. Menge, K. J. Nielsen, F. Chan, and T. C. Gouhier. 2019. Regional processes are stronger determinants of rocky intertidal community dynamics than local biotic interactions. Ecology 100:1–12.

Hanawa, K., and H. Mitsudera. Variation of water system distribution in the Sanriku coastal area. 1987. Journal of the Oceanographical Society of Japan 42: 435–446.

Hillebrand, H., I. Donohue, W. S. Harpole, D. Hodapp, M. Kucera, A. M. Lewandowska, J. Merder, J. M. Montoya, and J. A. Freund. 2020. Thresholds for ecological responses to global change do not emerge from empirical data. Nature Ecology and Evolution 4:1502–1509.

Hillebrand, H., S. Langenheder, K. Lebret, E. Lindström, Ö. Östman, and M. Striebel. 2018. Decomposing multiple dimensions of stability in global change experiments. Ecology Letters 21:21–30.

Holling, C. S., and G. K. Meffe. 1996. Command and control and the pathology of natural resource management. Conservation Biology 10:328–337.

Isoda, Y., and K. Suzuki. Interannual variations of the Tsugaru gyre. 2004. Bulletin of Fisheries Sciences, Hokkaido University 55: 71-74.

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

Japan Meteorological Agency. Fluctuations in the Kuroshio Current on a Scale of Months to Decades (Paths). http://www.data.jma.go.jp/gmd/kaiyou/data/shindan/b_2/kuroshio_stream/kuroshio_stream.html (in Japanese, accessed 11 March 2021).

Kanamori, Y., K. Fukaya, and T. Noda. 2017. Seasonal changes in community structure along a vertical gradient: patterns and processes in rocky intertidal sessile assemblages. Population Ecology 59:301–313.

Kawabe, M. 2005. Variations of the Kuroshio in the Southern Region of Japan: Conditions for large meander of the Kuroshio. Journal of Oceanography 61:529–537.

Kawajiri, M., T., Sasaki, and Y. Kageyama. 1981. Extensive deterioration of Ecklonia kelp stands and death of the plants, and fluctuations in abundance of the abalone off Toji, southern Izu peninsula. Bulletin of the Shizuoka Prefectural Fisheries Experiment Station 15: 19–30 (in Japanese).

Kéfi, S., V. Domínguez-García, I. Donohue, C. Fontaine, E. Thébault, and V. Dakos. 2019. Advancing our understanding of ecological stability. Ecology Letters 22:1349–1356.

Menge, B. A. 2000. Top-down and bottom-up community regulation in marine rocky intertidal habitats. Journal of Experimental Marine Biology and Ecology 250:1–26.

Menge, B. A., B. A. Daley, P. A. Wheeler, E. Dahlhoff, E. Sanford, and P. T. Strub. 1997. Benthic-pelagic links and rocky intertidal communities: Bottom-up effects on top-down control? Proceedings of the National Academy of Sciences of the United States of America 94:14530–14535.

Menge, B. A., T. C. Gouhier, S. D. Hacker, F. Chan, and K. J. Nielsen. 2015. Are meta-ecosystems organized hierarchically? A model and test in rocky intertidal habitats. Ecological Monographs 85:213–233.

Menge, B. A., J. Lubchenco, M. E. S. Bracken, F. Chan, M. M. Foley, T. L. Freidenburg, S. D. Gaines, G. Hudson, C. Krenz, H. Leslie, D. N. L. Menge, R. Russell, and M. S. Webster. 2003. Coastal oceanography sets the pace of rocky intertidal community dynamics. Proceedings of the National Academy of Sciences of the United States of America 100:12229–12234.

Moss, D. K., L. C. Ivany, E. J. Judd, P. W. Cummings, C. E. Bearden, W. J. Kim, E. G. Artruc, and J. R. Driscoll. 2016. Lifespan, growth rate, and body size across latitude in marine bivalvia, with implications for phanerozoic evolution. Proceedings of the Royal Society B: Biological Sciences 283: 20161364.

Mrowicki, R. J., N. E. O'Connor, and I. Donohue. 2016. Temporal variability of a single population can determine the vulnerability of communities to perturbations. Journal of Ecology 104:887–897.

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

Nielsen, K. J., and S. A. Navarrete. 2004. Mesoscale regulation comes from the bottom-up: Intertidal interactions between consumers and upwelling. Ecology Letters 7:31–41.

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

Noda, T., A. Iwasaki, and K. Fukaya. 2016. Recovery of rocky intertidal zonation: Two years after the 2011 Great East Japan Earthquake. Journal of the Marine Biological Association of the United Kingdom 96:1549–1555.

Noda, T., M. Sakaguchi, A. Iwasaki, and K. Fukaya. 2017. Influence of the 2011 Tohoku Earthquake on population dynamics of a rocky intertidal barnacle: cause and consequence of alteration in larval recruitment. Coastal Marine Science 40: 35–43.

Nomura, K., and I. Hirabayashi. 2018. Mass mortality of coral communities caused by abnormality low water temperature observed at Kii peninsula west coast for winter season in 2018. Marine Pavilion Supplement 7:1–14. (in Japanese).

Nuvoloni, F. M., R. J. F. Feres, and B. Gilbert. 2016. Species turnover through time: Colonization and extinction dynamics across metacommunities. American Naturalist 187:786–796.

Ohgaki, S. I., T. Kato, N. Kobayashi, H. Tanase, N. H. Kumagai, S. Ishida, T. Nakano, Y. Wada, and Y. Yusa. 2019. Effects of temperature and red tides on sea urchin abundance and species richness over 45 years in southern Japan. Ecological Indicators 96:684–693.

Ohtani, K. 1987. Westward inflow of the coastal Oyashio Water into the Tsugaru Strait. Bulletin of the Faculty of Fisheries Hokkaido University 38: 209–220 (in Japanese with English abstract).

Okuda, T., T. Noda, T. Yamamoto, N. Ito, and M. Nakaoka. 2004. Latitudinal gradient of species diversity: Multi-scale variability in rocky intertidal sessile assemblages along the Northwestern Pacific coast. Population Ecology 46:159–170.

Okunishi, T., S. Kakehi, D. Hasegawa, T. Tanaka, and K. Yokouchi. 2018. Characteristics of oceanographic condition of Tohoku prefecture in 2018. Bulletin of Liaison Conference of Tohoku Marine Surveys and Technology 68: 4–5 (in Japanese).

Pennekamp, F., M. Pontarp, A. Tabi, F. Altermatt, R. Alther, Y. Choffat, E. A. Fronhofer, P. Ganesanandamoorthy, A. Garnier, J. I. Griffiths, S. Greene, K. Horgan, T. M. Massie, E. Mächler, G. M. Palamara, M. Seymour, and O. L. Petchey. 2018. Biodiversity increases and decreases ecosystem stability. Nature 563:109–112.

Peterson, G., C. R. Allen, and C. S. Holling. 1998. Ecological resilience, biodiversity, and scale. Ecosystems 1:6–18.

Pimm, S.L. 1984. The complexity and stability of ecosystems. Nature 315:635–636.

Qiu, B. 2001. Kuroshio and Oyashio currents. In Ocean Currents: A Derivative of the Encyclopedia of Ocean Sciences (eds Steele, J. H. et al.) Academic Press, Cambridge, pp.1413–1425.

Qiu, B. 2002. Large-scale variability in the midlatitude subtropical and subpolar North Pacific Ocean: Observations and causes. Journal of Physical Oceanography 32:353–375.

Radchuk, V., F. De Laender, J. S. Cabral, I. Boulangeat, M. Crawford, F. Bohn, J. De Raedt, C. Scherer, J. C. Svenning, K. Thonicke, F. M. Schurr, V. Grimm, and S. Kramer-Schadt. 2019. The dimensionality of stability depends on disturbance type. Ecology Letters 22:674–684.

Raffaelli, D, and S.J. Hawkins. 1996. Intertidal ecology. Springer Science & Business Media, Berlin.

Sahara, R., K. Fukaya, T. Okuda, M. Hori, T. Yamamoto, M. Nakaoka, and T. Noda. 2016. Larval dispersal dampens population fluctuation and shapes the interspecific spatial distribution patterns of rocky intertidal gastropods. Ecography 39:487–495.

Sakurai, Y. 2007. An overview of the Oyashio ecosystem. Deep-Sea Research Part II: Topical Studies in Oceanography 54:2526–2542.

Sanford, E. 1999. Regulation of keystone predation by small changes in ocean temperature. Science 283:2095–2097.

Schoch, G. C., B. A. Menge, G. Allison, M. Kavanaugh, S. A. Thompson, and S. A. Wood. 2006. Fifteen degrees of separation: Latitudinal gradients of rocky intertidal biota along the California Current. Limnology and Oceanography 51:2564–2585.

Takami, H., T. Saido, T. Endo, T. Noro, T. Musashi, and T. Kawamura. 2008. Overwinter mortality of young-of-the-year Ezo abalone in relation to seawater temperature on the north Pacific coast of Japan. Marine Ecology Progress Series 367:203–212.

Takasugi, S. 1992. Distribution of Tsugaru Warm Current water in the Iwate coastal area and their influence to sea surface temperature at coastal hydrographic station. Bulletin of the Japanese Society of Fisheries Oceanography 56: 434–448 (in Japanese with English abstract).

Takasugi, S. and I. Yasuda. Variation of the Oyashio water in the Iwate coastal region and in the vicinity of east coast of Japan. 1994. Bulletin of the Japanese Society of Fisheries Oceanography 58: 253–259 (in Japanese with English abstract).

Taniguchi, K., M. Sato, and K.Owada. On the characteristics of the structural variation in the Eisenia bicyclis population on Joban coast, Japan. 1986. Bulletin of Tohoku National Fisheries Researh Institute 48: 49–57 (in Japanese with English abstract).

Thrush, S. F., J. E. Hewitt, P. K. Dayton, G. Coco, A. M. Lohrer, A. Norkko, J. Norkko, and M. Chiantore. 2009. Forecasting the limits of resilience: Integrating empirical research with theory. Proceedings of the Royal Society B: Biological Sciences 276:3209–3217.

Tilman, D., P. B. Reich, and J. M. H. Knops. 2006. Biodiversity and ecosystem stability in a decade-long grassland experiment. Nature 441:629–632.

Tsujino, M., M. Hori, T. Okuda, M. Nakaoka, T. Yamamoto, and T. Noda. 2010. Distance decay of community dynamics in rocky intertidal sessile assemblages evaluated by transition matrix models. Population Ecology 52:171–180.

Vinueza, L. R., B. A. Menge, D. Ruiz, and D. M. Palacios. 2014. Oceanographic and climatic variation drive top-down/bottom-up coupling in the Galápagos intertidal meta-ecosystem. Ecological Monographs 84:411–434.

Yamaguchi, M. 1986. Acanthaster planci infestations of reefs and coral assemblages in Japan: a retrospective analysis of control efforts. Coral Reefs 5:23–30.

Yatsu, A., S. Chiba, Y. Yamanaka, S. I. Ito, Y. Shimizu, M. Kaeriyama, and Y. Watanabe. 2013. Climate forcing and the Kuroshio/Oyashio ecosystem. ICES

Journal of Marine Science 70:922–933.

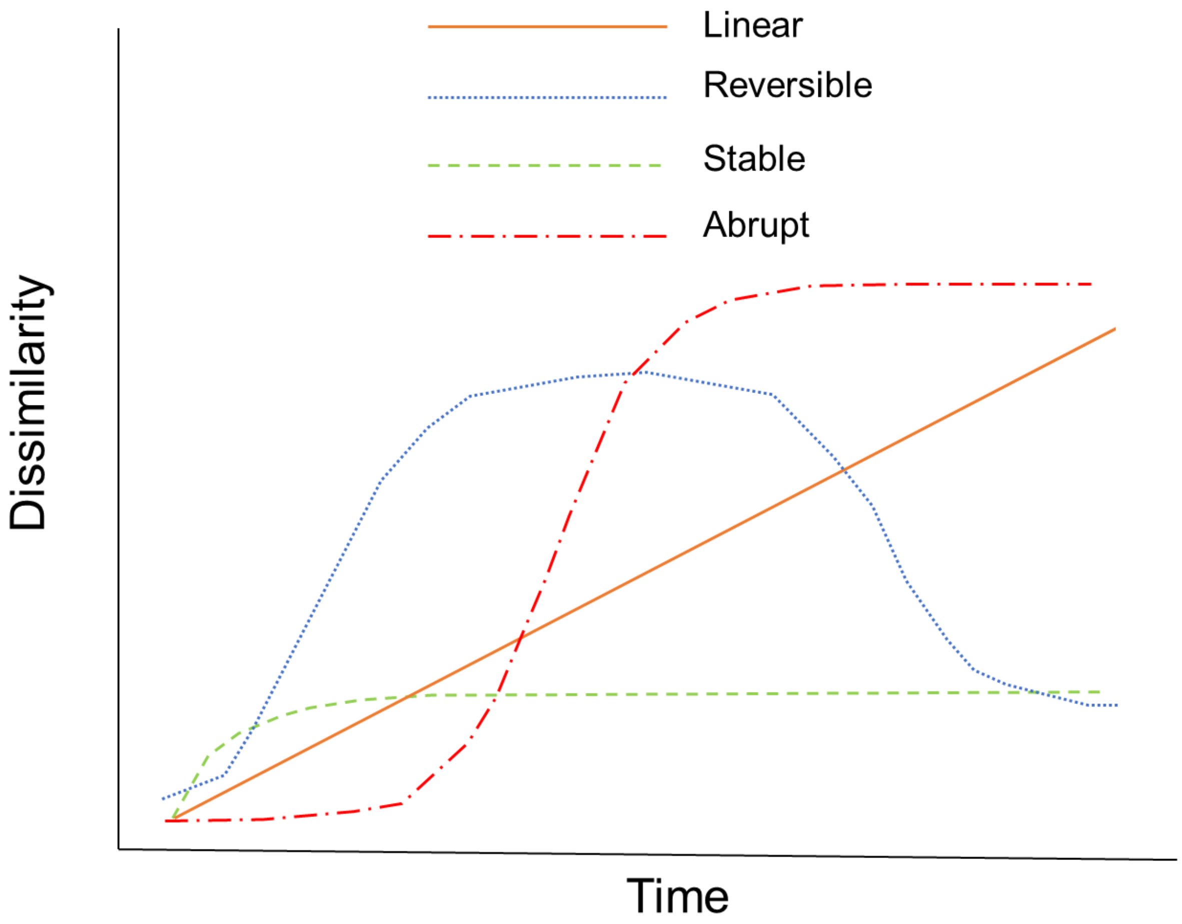


Fig. 2-1. Conceptual diagram of four trajectories of community change (Bagchi et al. 2017). The *y*-axis represents the dissimilarity index of species composition between an initial time and each subsequent time. Each trajectory represents a different concept of community ecological resilience.

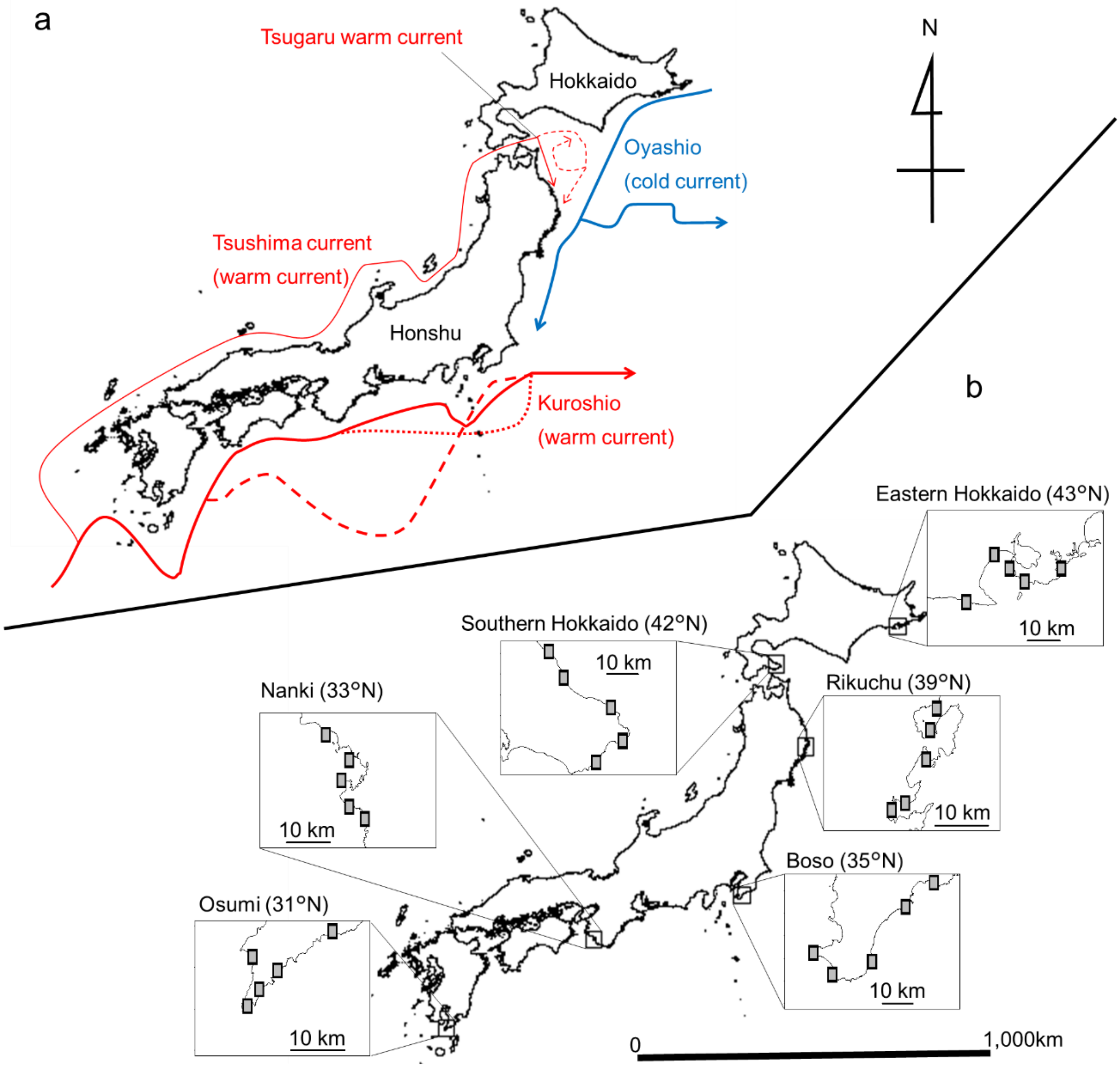


Fig. 2-2. Maps showing (a) major ocean current systems around Japan, and (b) the six study regions along the Northwestern Pacific coast of Japan between 31°N and 43°N. Five rocky shores (shaded squares) were chosen for the census of intertidal sessile organisms in each region. The red solid and broken lines in (a) show alternative current paths. This figure was generated with R version 3.5.2 and the GADM database (www.gadm.org), version 2.5.

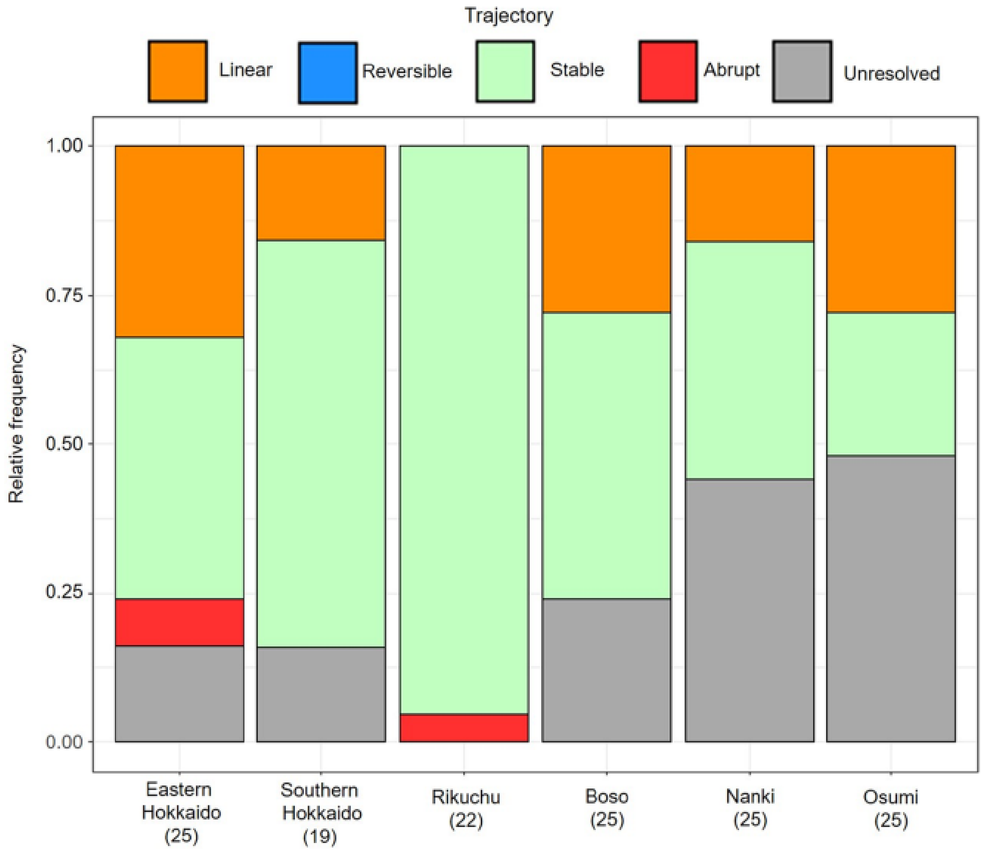


Fig. 2-3. Relative frequencies of trajectories representing the patterns of ecological resilience of rocky intertidal sessile communities along the Pacific coast of Japan, based on the Sørensen dissimilarity index. Also shown are the relative frequencies of instances where trajectories could not be reliably classified (i.e., "unresolved"). The numbers of plots in each region are in parentheses.

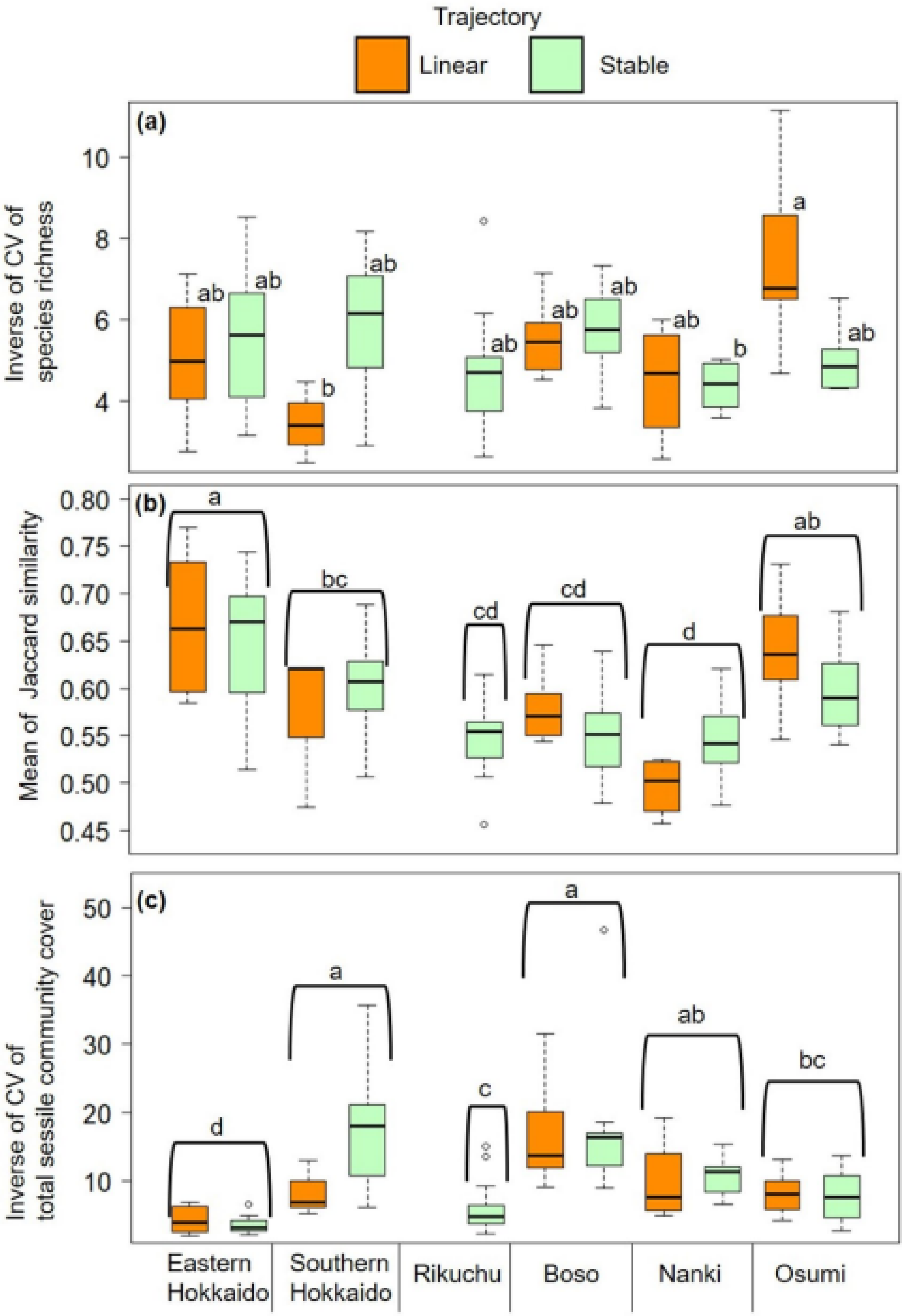


Fig. 2-4. Box plots of the temporal invariability of (a) species richness, (b) species composition, and (c) community abundance. Box plots show the median, minimum, maximum, and first and third quartiles. Different letters indicate statistical differences in post hoc Bonferroni pairwise comparisons at $P < 0.05$.

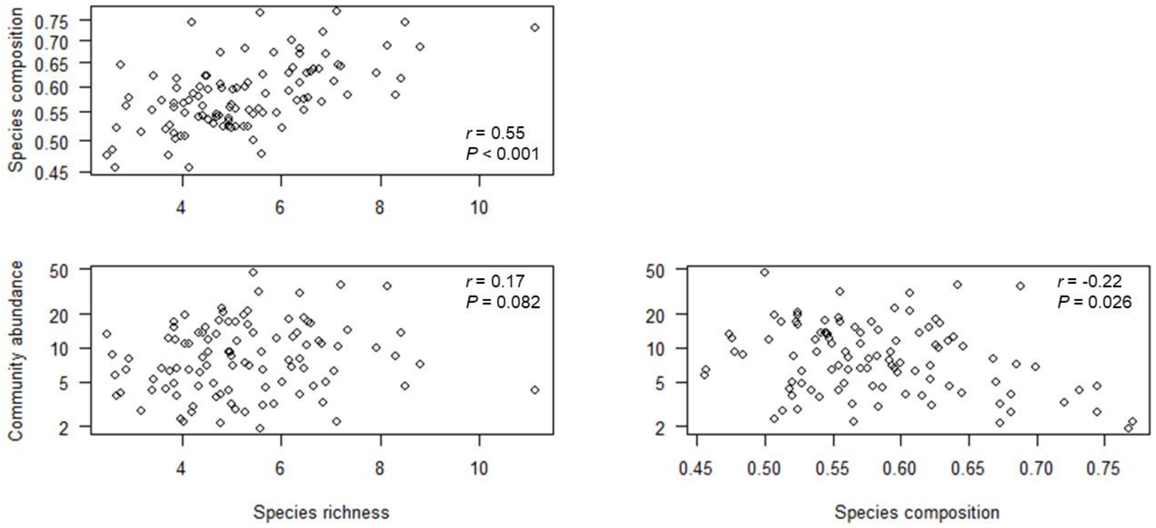


Fig. S2-1. Spearman rank correlation coefficients (r) for the relationships between three measures of community temporal invariability.

Table 2-1. Four community trajectories used in this study and their corresponding concepts of ecological resilience as quantitatively identified by Bagchi et al. (2017).

Community trajectory	Description	Corresponding concepts of ecological resilience
Linear	Slow, incremental change with time	Nonequilibrium, phase shift
Reversible	Major changes, with return to original state	Engineering resilience
Stable	No appreciable change over time	Resistance, or asymptotic state
Abrupt	Relatively sudden change	State transition, threshold, regime shift, tipping point

Table 2-2. Summary of model coefficients (mean ± SD) for each trajectory found for communities of rocky intertidal sessile organisms in six regions along the Pacific coast of Japan. Different superscript letters signify statistically significant differences as shown by post hoc Bonferroni pairwise comparisons ($P < 0.05$). NA (not available) indicates that a trajectory was not applicable in a particular region.

Region	Linear	Stable	Abrupt
Eastern Hokkaido	$\alpha = 0.014^{ab} \pm 0.004$	$\varphi_1 = 0.34^{bc} \pm 0.09$ $\varphi_2 = -0.69^{a} \pm 0.45$	$\delta = 0.26 \pm 0.09$ $\theta = 2.32 \pm 0.62$ $\varphi = 1.34 \pm 0.09$
Southern Hokkaido	$\alpha = 0.012^{ab} \pm 0.004$	$\varphi_1 = 0.32^{c} \pm 0.04$ $\varphi_2 = -0.92^{ab} \pm 0.36$	NA
Rikuchu	NA	$\varphi_1 = 0.48^{a} \pm 0.06$ $\varphi_2 = -0.66^{a} \pm 0.47$	$\delta = 0.41 \pm 0$ $\theta = 1.62 \pm 0$ $\varphi = 0.66 \pm 0$
Boso	$\alpha = 0.012^{ab} \pm 0.006$	$\varphi_1 = 0.39^{bc} \pm 0.05$ $\varphi_2 = -0.83^{ab} \pm 0.34$	NA
Nanki	$\alpha = 0.017^{a} \pm 0.003$	$\varphi_1 = 0.41^{ab} \pm 0.06$ $\varphi_2 = -1.29^{b} \pm 0.29$	NA
Osumi	$\alpha = 0.008^{b} \pm 0.002$	$\varphi_1 = 0.39^{abc} \pm 0.09$ $\varphi_2 = -1.41^{b} \pm 0.54$	NA

Table 2-3. Results of multiple regression analysis for the effects of current systems and strength of current fluctuations on model coefficients of each trajectory type (linear [α]; stable [ϕ_1, ϕ_2]) and on three measures of community temporal invariability (species richness, species composition, and community abundance). Columns report the estimated coefficients for explanatory variables, their standard errors, t-values and *P*-values.

Response variable	Explanatory variable	Estimate	Std. Error	t-value	*P*
Linear α	Intercept	0.0057	0.0026	2.19	0.0377
	Current systems	0.0037	0.0019	1.94	0.0639
Transformation: none	Current fluctuation	0.0033	0.0013	2.59	0.0157
Stable φ_1	Intercept	0.2785	0.0288	9.66	<0.001
	Current systems	-0.0024	0.0188	-0.13	0.9000
Transformation: none	Current fluctuation	0.0553	0.0116	4.78	<0.001
Stable φ_2	Intercept	-1.1808	0.1691	-6.99	<0.001
	Current systems	0.3777	0.1100	3.44	<0.001
Transformation: none	Current fluctuation	0.0281	0.0679	0.41	0.6804
Species richness	Intercept	0.8254	0.0349	23.67	<0.001
	Current systems	-0.0415	0.0241	-1.72	0.0886
Transformation: $\log_{10}$	Current fluctuation	-0.0499	0.0148	-3.37	0.0011
Species composition	Intercept	-0.1749	0.0110	-15.85	<0.001
	Current systems	0.0223	0.0076	2.92	0.0043
Transformation: $\log_{10}$	Current fluctuation	-0.0360	0.0047	-7.69	<0.001
Community abundance	Intercept	0.8981	0.0808	11.12	<0.001
	Current systems	-0.2539	0.0559	-4.54	<0.001
Transformation: $\log_{10}$	Current fluctuation	0.0693	0.0343	2.02	0.0461

Table 2-4. Results of two-way ANOVA for the effects of region and trajectory (linear or stable)[a] on three measures of community temporal invariability (species richness (a), species composition (b), and community abundance (c)).

Source of variation	df	MS	*F*	*P*
(a) Species richness				
Region	5	0.05431	4.209	0.00174
Trajectory[a]	1	0.00417	0.323	0.57113
Region × Trajectory	4	0.05376	4.166	0.00383
Residuals	91	0.01291		
Transformation: $\log_{10}$				
Levene's test: F =1.7328, P > 0.05				
(b) Species composition				
Region	5	0.020171	13.978	<0.001
Trajectory[a]	1	0.000529	0.366	0.5464
Region × Trajectory	4	0.002939	2.037	0.0958
Residuals	91	0.001443		
Transformation: $\log_{10}$				
Levene's test: F = 1.5378, P > 0.05				
(c) Community abundance				
Region	5	1.1666	29.392	<0.001
Trajectory[a]	1	0.0213	0.537	0.465
Region × Trajectory	4	0.0684	1.725	0.151
Residuals	91	0.0397		
Transformation: $\log_{10}$				
Levene's test: F = 0.7907, P > 0.05				

[a] Please see main text for a description of community trajectories.

Table S2-1. Results of ANOVAs for the effect of region on model coefficients of each trajectory type (linear [a], stable [b and c]) of rocky intertidal sessile communities in six regions along the Pacific coast of Japan.

Source of variation	df	MS	*F*	*P*
(a) α, coefficient of the linear trajectory				
Region	4	0.00006155	3.163	0.032
Residuals	24	0.00001946		
Transformation: none				
Levene's test: $F = 1.9349$, $P > 0.05$				
(b) φ_1, coefficient of the stable trajectory				
Region	5	0.05187	11.49	<0.001
Residuals	67	0.00451		
Transformation: none				
Levene's test: $F = 0.5406$, $P > 0.05$				
(c) φ_2, coefficient of the stable trajectory				
Region	5	0.9775	5.364	<0.001
Residuals	67	0.1822		
Transformation: none				
Levene's test: $F = 0.7071$, $P > 0.05$				

Table S2-2. Frequency of occurrence of each sessile organism in each region. The frequency of occurrence was calculated as the number of census where each sessile organism was recorded within each region/ total number of census investigated at each region × 100 (%).

Phylum, Kingdom and Domain	Taxon	Region					
		Eastern Hokkaido	Southern Hokkaido	Rikuchu	Boso	Nanki	Osumi
Bacteria							
Cyanobacteria	Cyanophyceae spp.	-	16.83	48.43	43.32	59.50	45.00
Eukarya							
Plantae							
Rhodophyta	*Acrosorium yendoi*	-	8.58	3.70	-	-	-
	Ahnfeltiopsis flabelliformis	-	-	5.13	-	-	-
	Bostrychia tenella	-	-	-	-	-	2.25
	Caulacanthus ustulatus	-	22.11	44.73	95.97	78.25	79.75
	Chondracanthus intermedius	-	-	23.65	96.47	44.75	50.75
	Chondria crassicaulis	-	16.83	21.65	4.28	-	-
	Chondrophycus undulata	-	-	-	6.55	7.75	18.25
	Chondrus elatus	-	-	5.98	-	-	-
	Chondrus nipponicus	-	-	6.27	-	-	-
	Chondrus ocellatus	-	-	5.98	3.27	10.50	-
	Chondrus spp.	-	-	-	3.78	5.75	4.25
	Chondrus verrucosus	-	-	18.23	47.61	4.25	2.25
	Chondrus yendoi	94.44	53.47	49.29	-	-	-
	Congregatocarpus pacificus	5.05	-	-	-	-	-
	Corallina pilulifera	94.70	71.29	13.68	65.74	4.50	17.50
	Corallinales spp.	5.30	78.88	90.60	99.50	99.00	99.00
	Dermonema pulvinatum	-	-	-	13.85	9.25	-
	Dumontia simplex	-	8.25	-	-	-	-
	Gelidium divaricatum	-	-	22.79	8.31	33.50	57.00
	Gloiopeltis furcata	93.94	95.05	50.71	-	-	-
	Grateloupia spp.	-	-	-	-	6.25	-
	Hildenbrandia spp.	36.11	93.07	92.88	10.83	98.00	98.00
	Jania adhaerens	-	-	-	-	8.00	9.25
	Laurencia okamurae	-	-	5.98	58.94	4.00	30.75
	Laurencia spp.	-	-	-	3.27	5.75	5.25
	Lomentaria hakodatensis	-	12.54	8.55	-	-	-
	Mastocarpus pacificus	14.14	41.91	-	-	-	-
	Mazzaella japonica	-	7.59	-	-	-	-
	Nemalion vermiculare	-	8.91	7.12	-	-	-
	Neorhodomela aculeata	4.29	3.96	-	-	-	-
	Neorhodomela oregona	12.88	-	-	-	-	-
	Neodilsea yendoana	-	6.27	-	-	-	-
	Neosiphonia yendoi	57.58	10.56	3.13	-	-	-
	Odonthalia corymbifera	3.03	-	-	-	-	-
	Palisada yamadana	-	-	-	-	-	4.00
	Palmaria palmata	-	5.61	-	-	-	-
	Peyssonnelia conchicola	-	-	-	17.63	19.50	15.00
	Polyopes affinis	4.04	15.84	27.07	-	2.75	-
	Polyopes prolifer	-	-	6.84	8.31	-	-
	Polysiphonia spp.	-	5.61	3.70	5.29	-	-
	Porphyra yezoensis	-	6.60	-	-	-	-
	Pterocladiella tenuis	-	-	5.13	7.05	18.25	7.50
	Pterosiphonia bipinnata	17.93	-	-	-	-	-
	Ptilota filicina	7.07	2.97	-	-	-	-
	Rhodellophyceae spp.	-	-	-	3.78	12.75	5.75

Table S2-2. Continued

Phylum, Kingdom and Domain	Taxon	Region					
		Eastern Hokkaido	Southern Hokkaido	Rikuchu	Boso	Nanki	Osumi
Chlorophyta	*Boodlea coacta*	-	-	-	27.46	8.50	27.50
	Chaetomorpha aerea	16.92	64.69	11.40	-	-	-
	Chaetomorpha moniligera	7.32	32.01	-	-	-	-
	Cladophora herpestica	-	-	-	-	-	6.50
	Cladophora opaca	56.57	69.97	56.70	-	-	-
	Cladophora spp.	-	-	9.69	13.85	8.75	16.25
	Codium fragile	-	2.64	-	-	-	-
	Collinsiella cava	-	-	-	-	7.00	-
	Palmophyllum spp.	-	-	-	-	2.25	-
	Ulva pertusa	64.65	61.39	15.38	-	-	-
	Ulva spp1.(It used to be accepted as Enteromorpha spp.)	4.29	15.18	4.56	62.22	47.00	21.00
	Ulva spp2.	-	-	-	74.56	43.25	69.50
	Ulvella spp.	-	-	-	-	70.50	82.00
	Valonia spp.	-	-	-	-	2.50	-
Ochrophyta	*Alaria crassifolia*	-	5.94	-	-	-	-
	Alaria praelonga	4.80	-	-	-	-	-
	Analipus japonicus	96.72	88.78	60.40	-	-	-
	Bacillariophyceae spp.	3.28	11.88	-	18.89	6.00	4.25
	Ceramium spp.	-	-	-	2.27	2.25	4.50
	Colpomenia bullosa	16.16	8.58	-	-	-	-
	Colpomenia sinuosa	-	-	3.99	4.03	8.25	-
	Dictyopteris pacifica	-	2.31	-	-	-	-
	Dictyota dichotoma	-	19.14	6.84	6.05	-	-
	Endoplura aurea	-	-	40.74	63.73	-	-
	Fucus evanescens	31.82	6.27	-	-	-	-
	Ishige okamurae	-	-	-	71.03	33.75	39.00
	Ishige sinicola	-	-	-	38.79	-	-
	Leathesia marina	39.90	58.42	5.13	15.62	8.50	-
	Melanosiphon intestinalis	20.45	23.76	-	-	-	-
	Myelophycus simplex	-	-	-	15.11	-	2.75
	Neoralfsia expansa	-	-	-	-	52.25	23.00
	Petalonia binghamiae	3.03	3.30	-	-	-	-
	Petrospongium rugosum	-	-	-	20.40	-	-
	Phaeophyceae spp.	-	27.06	58.97	38.79	67.50	83.00
	Ralfsia verrucosa	-	42.90	21.08	-	-	-
	Saccharina japonica var. japonica	-	4.95	-	-	-	-
	Sargassum fusiforme	-	-	11.97	53.40	23.25	-
	Sargassum thunbergii	-	28.71	5.70	6.30	-	-
	Scytosiphon lomentaria	3.03	7.92	-	-	-	-
	Silvetia babingtonii	-	25.08	-	-	-	-
	Sphacelaria spp.	25.25	19.14	3.42	-	-	-
Tracheophyta	*Phyllospadix iwatensis*	-	9.90	-	-	-	-

Table S2-2. Continued

Phylum, Kingdom and Domain	Taxon	Region					
		Eastern Hokkaido	Southern Hokkaido	Rikuchu	Boso	Nanki	Osumi
Animalia							
Porifera	*Halichondria okadai*	-	-	-	22.67	5.50	4.00
	Halichondria panicea	4.80	6.93	11.40	19.65	14.75	53.00
	Haliclona permollis	-	-	-	-	-	21.75
	Haliclona spp.	-	-	-	36.52	3.75	15.75
	Hymeniacidon sinapium	-	-	4.56	2.52	5.25	16.75
Cnidaria	*Actinia equina*	-	25.41	-	6.05	-	-
	Anthopleura kurogane	-	4.29	-	-	-	-
	Anthopleura uchidai	-	15.18	26.78	74.81	7.75	10.25
	Campanulariidae spp.	-	-	7.41	-	-	-
	Cnidopus japonicus	14.14	11.88	-	-	-	-
	Dynamena crisioides	-	-	-	-	11.25	18.50
	Haliplanella lineata	-	-	-	-	7.50	7.75
Mollusca	*Acar plicata*	-	-	-	3.78	-	-
	Arca boucardi	-	-	-	3.27	5.25	-
	Arcidae spp.	-	-	-	4.03	7.75	10.25
	Cardita leana	-	-	-	4.28	-	-
	Chama sp.	-	-	-	-	13.00	-
	Crassostrea gigas	-	-	49.57	-	6.75	3.50
	Hormomya mutabilis	-	-	-	8.56	-	-
	Isognomon nucleus	-	-	-	-	-	4.50
	Mytilus coruscus	-	3.63	14.25	-	-	-
	Mytilus galloprovincialis	-	-	35.33	-	-	-
	Mytilus trossulus	6.57	22.44	-	-	-	-
	Pinctada martensii	-	-	-	-	-	2.25
	Saccostrea kegaki	-	-	10.54	4.03	42.00	41.00
	Saccostrea mordax	-	-	-	-	40.50	70.75
	Septifer bilocularis	-	-	-	16.12	36.75	64.50
	Septifer virgatus	-	45.21	60.68	-	5.50	30.75
	Serpulorbis imbricatus	-	-	-	21.66	15.50	25.75
	Xenostrobus atratus	-	-	-	-	15.75	-
Annelida	*Hydroides ezoensis*	-	18.81	87.46	9.82	-	-
	Neodexiospira spirillum	18.69	33.33	39.60	-	-	-
	Neodexiospira spp.	-	-	-	69.77	13.00	18.25
	Polychaeta spp.	-	-	-	-	-	19.25
	Pseudopotamilla occelata	-	9.90	15.38	-	-	-
	Sabellidae spp.	-	-	-	-	-	9.00
	Serpulidae spp.	-	-	-	11.84	27.25	39.25
	Spirobranchus kraussii	-	-	-	69.27	83.50	57.50
Arthropoda	*Amphibalanus amphitrite*	-	-	-	-	-	3.00
	Balanus glandula	58.08	31.68	58.40	-	-	-
	Capitulum mitella	-	-	7.69	3.27	52.25	69.25
	Chthamalus challengeri	-	96.70	86.61	51.39	79.00	59.00
	Chthamalus dalli	96.97	-	-	-	-	-
	Corophium sp.	13.64	6.60	-	-	-	-
	Perforatus perforatus	-	-	6.55	-	-	-
	Semibalanus cariosus	18.94	46.53	32.76	-	-	-
	Tetraclita japonica	-	-	-	2.77	57.00	60.50
	Tetraclita squamosa	-	-	-	-	13.00	40.25
Bryozoa	Hippothoidae spp.	2.78	-	-	-	-	-
	Membraniporidae spp.	-	-	2.56	-	-	-
	Microporellidae spp.	6.82	3.30	17.09	-	-	-
	Vesiculariidae spp.	2.53	-	-	-	-	-
	Watersipora cucullata	-	-	27.07	5.54	4.50	9.00
Chordata	Botryllidae spp.	-	-	3.42	-	-	-
	Didemnidae spp.	-	-	-	-	-	5.50
	Polycitor proliferus	-	-	-	13.60	-	8.50
	Pyura vittata	-	-	11.40	-	-	-

Chapter 3

The responses of rocky intertidal communities in the southeast Hokkaido to marine heatwaves during 2010–2016

3.1. Introduction

Marine heatwaves (MHWs) are anomalous, sea-surface-temperature warm events and are defined as when an upper determined threshold (the 90th percentile of temperature relative to the long-term climatology) is exceeded for five or more days (Hobday et al. 2016). MHWs are known to sometimes persist for long periods (year-round) (Hobday et al. 2018) or to recur annually for short periods (e.g., every summer) (Miyama et al. 2021a, b). Category I–IV MHWs are defined on the basis of the degree to which sea surface temperatures exceed the local climatology (Hobday et al. 2018). From 1925 to 2016, MHW frequency and duration increased by 34% and 17%, respectively, with a 54% increase globally in annual marine heatwave days (Oliver et al. 2018). Also, the number of MHW days is projected to further increase as a result of global warming (Frölicher et al. 2018). Therefore, there is an urgent need to understand the response of marine organisms to MHWs.

In elucidating the response of marine ecosystems to MHWs, it is important to focus on revealing the impacts of MHWs on functional groups and species niche traits for various habitats, organisms, and regions. This is because understanding the differences in responses to MHWs by functional group will lead to a better understanding of the effects of MHWs at the community and ecosystem level. In addition, the relationship between species niche traits such as thermal tolerance and species' responses to MHWs is important because it will lead to an understanding of the physiological and ecological processes behind differences between species in MHW effects.

The effects of MHWs on marine ecosystems have been reported for various parts of the world such as the Mediterranean, Northeast Pacific, and western Australia (Hobday et al. 2018; Smale et al. 2019). These studies have shown that biological responses to MHWs are diverse (negative, positive, or neutral) across multiple trophic levels (i.e., lower to upper trophic levels) and taxonomic groups (e.g., plankton, algae, invertebrates, fishes, birds, and mammals) (Ruthrof et al. 2018; Sanford et al. 2019; Smale et al. 2019; Suryan et al. 2021). The effects of MHWs vary among species: the abundances of cold-affinity species decreased after one MHW (Smale et al.2017) and those of warmer-water species increased (Smale et al. 2017; Sanford et al. 2019; Miner et al. 2021) for herbivorous invertebrates (sea urchins and gastropods), barnacles and Rhodophyta. Many studies have reported differences in the response of different functional groups to MHWs (Wernberg et al. 2013; Smale and Wernberg. 2013; Smale et al. 2019; Suryan et al. 2021; Weitzman et al. 2021), and there are also reported cases of indirect spillover of MHW effects to other functional groups (Wernberg et al. 2013; Smale and Wernberg. 2013; Smale et al. 2017). For example, the decline in abundance of herbivorous macroinvertebrates (sea urchins and gastropods) after the 2011 MHW in western Australia is possibly because, in addition to direct thermal stress, invertebrate populations were also likely affected by the indirect effects of loss of habitat and food resources (Smale et al. 2017). Responses to an MHW can vary regionally. For example, in the warm regions along the west coast of Australia, the community structures of algae (Wernberg et al. 2013; Smale and Wernberg. 2013), invertebrates (Wernberg et al. 2013) and fishes (Wernberg et al. 2013), and the abundances of herbivorous macroinvertebrates (Smale et al. 2017) were significantly different after the 2011 MHW, whereas no effects were detected in the cooler regions.

Despite the many studies that have been conducted in recent years, little is known about how MHWs have impacted marine organisms and these studies are lacking from several perspectives. First, most previous studies have evaluated the impact of heat waves using comparisons of abundances from several surveys before and after an MHW (Smale and Wernberg. 2013; Wernberg et al. 2013; Smale et al. 2017; Sanford et al. 2019; Thomsen et al. 2019; Weitzman et al. 2021). Therefore, the estimated impacts of MHWs on abundances include not only the direct effects of MHWs, but also the effects of environmental stochasticity other than the MHWs. Second, accumulative carryover effects—that is, those occurring when the effects of sequential events accumulate over time (Ryo et al. 2019)—may result when MHW events persist for several years or occur repeatedly over a short period (Hobday et al. 2018; Miyama et al. 2021a, b). However, the accumulative carryover effects of MHWs on organisms are largely unknown. Third, there has been little investigation of the relationship between species niche traits and susceptibility to MHWs, other than for the thermal niche traits of individual species (Smale et al. 2017; Sanford et al. 2019; Miner et al. 2021).

The rocky intertidal zone is a habitat where the intensity of desiccation stress varies widely over a narrow vertical range (Noda. 2009). The rocky intertidal zone is inhabited by species of various trophic levels, including algae, sessile animals, grazers and carnivores (Okuda et al. 2010; Iwasaki et al. 2016), and each species inhabits a specific elevation range depending on its desiccation tolerance, with the more desiccation-tolerant species generally being found in the upper intertidal zone. Rocky intertidal communities are some of the best study systems for assessing the response of marine benthic communities to MHWs. First, the component species of rocky intertidal communities have a variety of trophic levels. Second, the abundance of most species can accurately be quantified in a non-destructive way. Therefore, it is relatively easy to continuously obtain highly accurate time-series data for the abundance of community component species before and after MHWs.

Relatively few previous studies have described the effects of MHWs on rocky intertidal communities, with one case in the South Island of New Zealand in 2017–2018 (Thomsen et al. 2019) and another in the northeast Pacific during 2014–2016 (Sanford et al. 2019; Miner et al. 2021; Suryan et al. 2021; Weitzman et al. 2021, Spiecker and Menge. 2022). The impact of MHWs on rocky intertidal organisms was relatively well documented in the latter series of studies, which have revealed that the effects of MHWs vary by functional group. For example, the abundance of macroalgae (*Fucus*) and that of predatory invertebrates (sea stars) declined precipitously after the onset of the MHW; in contrast, the abundance of sessile invertebrates (mussels) increased (Suryan et al. 2021). In addition, algae cover (*Fucus* and other fleshy macroalgae) declined during and after the MHW, whereas that of sessile animals (barnacles and mussels) increased (Weitzman et al. 2021). The effects of MHWs may also differ among species depending on their thermal niche, with the geographic distributions of southern species shifting northwards with striking increases in recruitment (Sanford et al. 2019). In these studies, however, the effects of MHWs on abundance are estimated by methods that cannot isolate the effects of MHWs from overall environmental stochasticity, so the estimates are not highly accurate.

Differences in response to an MHW by functional group have also been reported in rocky intertidal communities (Suryan et al. 2021; Weitzman et al. 2021), but so far the differences in response using the abundance of an entire functional group have not been evaluated. Also not yet evaluated are the presence and extent of accumulative carryover effects of MHWs. Furthermore, the relationship between the vertical niches of sessile organisms as a species niche trait and susceptibility to MHWs has never been investigated. Among rocky intertidal sessile organisms, species with higher vertical niches may be less susceptible to the effects of anomalous sea surface warming due to MHWs. This is because the upper intertidal zone has a shorter immersion period than the lower intertidal zone, and thermal variation and extremes increase from low to high elevations in intertidal habitats (Beneditti-Cetti et al. 2006; Watt and Scrosati. 2013).

In the summer (July–September) of all years from 2010 to 2016, MHWs classified as category I or II occurred in the Oyashio water off southeast Hokkaido, northern Japan (Miyama et al. 2021a, b). The sea surface temperature in summer of all of these years was continuously higher by more than 1°C than its climatology, 17.5°C, as defined for the period between 1993 and 2009, and the average summer sea surface temperature between 2010 and 2016 was 18.9°C (Fig. 3-1; Miyama et al. 2021a). The MHW events have been attributed to a weakening of the influence from cold Oyashio water resulting from an increase in anticyclonic eddies from the warm Kuroshio Extension (Miyama et al. 2021a, b). After the end of this series of MHWs, sea surface temperatures declined to normal in 2017 and 2018 (Fig. 3-1; Miyama et al. 2021a, b). Subsequently, anticyclonic eddies returned in 2019 and 2020, and sea surface temperatures again increased (Miyama et al. 2021b). In this study, I examined the impacts of the MHWs that occurred in southeastern Hokkaido from 2010 to 2016 on community abundance (i.e., the sum of the abundances of all species in the community) of the four main functional groups of rocky intertidal communities and on the abundances of individual species during the MHWs from 2010 to 2016 and for two years after the end of the MHWs (when sea surface temperatures were at normal levels). I estimated the effect size of the MHWs at the regional scale, thereby eliminating the other effects of environmental stochasticity on the community abundance and the abundance of individual species.

I included only two years after the MHWs (2017 and 2018) for evaluation; the marine conditions in the study area were far from normal in the three subsequent years because anticyclonic eddies again raised sea surface temperatures in 2019 and 2020 (Miyama et al. 2021b), and in 2021 there was an outbreak of harmful algae (Misaka and Ando.2021; Iwataki et al. 2022). I specifically asked the following questions: (1) Did MHWs have accumulative carryover effects at the regional scale on the community abundance of the four functional groups and the abundance of individual species? (2) How did the effects of the MHWs on these community abundances at the regional scale differ between the MHWs (2010–2016) and the subsequent recovery in the first two years afterward (2017 and 2018)? (3) How did the impacts of MHWs on the abundance of each species at the regional scale during the MHWs (2010–2016), and in the first (2017) and second (2018) years after the MHWs differ depending on species niches traits (thermal and vertical niches)? I assessed the effects of MHWs at the regional scale because the thermal environment is expected to have large spatial variation within the range encompassing the metapopulation scale of marine benthos (Helmuth et al.2002, 2006).

3.2. Materials and methods

Study area

The study area is located on the coast along the Northwest Pacific Ocean in southeast Hokkaido, Japan (Fig. 3-2). The area is within the cold temperate provinces (Spalding et al. 2007) and is impacted by the cold Oyashio current (Payne et al. 2012; Ishida et al. 2021; Miyama et al. 2021a, b). In the study area, the mid-tidal zone is dominated by the native barnacle *Chthamalus dalli* and perennial seaweeds such as the crustose coralline alga *Corallina pilulifera*, the red algae *Gloiopeltis furcata* and *Chondrus yendoi*, and the brown alga *Analipus japonicus* (Kanamori et al. 2017; Ishida et al. 2021). Invertebrate predators include the whelk *Nucella lima* and the starfish *Leptasterias ochotensis* (Noda and Ohira. 2020). The invasive barnacle *Balanus glandula* invaded this area in 2004, but it did not become a dominant species, with an average cover of less than 5% (Noda and Ohira. 2020). There was a massive harmful algal bloom in this region during September–November 2021 (Misaka and Ando. 2021; Iwataki et al. 2022). The dominant species of the bloom was identified as *Karenia selliformis* (Gymnodiniales, Dinophyceae) (Iwataki et al. 2022). Misaka and Ando (2021) have reported on the mortality of marine organisms such as salmon, sea urchins, whelks, octopuses, and Sipuncula caused, by the bloom.

Census design

I used hierarchical nested sampling (Noda. 2004) for the layout of each site. Five rocky shores were chosen for the census of intertidal organisms along the coast in southeast Hokkaido, Japan, by the Northwest Pacific Ocean (Fig. 3-2). Within each shore, I established four or five permanent census plots (the total number of plots was 21) on steep rock walls in semi-exposed locations. Each plot was 50 cm wide by 100 cm high, with the vertical midpoint corresponding to mean tidal level. Abundances of all sessile organisms (macroalgae and sessile invertebrates) were determined by placing 200 grid points at 5-cm intervals both vertically and horizontally on the rock surface within each census plot and identifying and recording the species occupying each grid point. The abundances of all mobile organisms (herbivorous and carnivorous invertebrates) were recorded as the number of individuals of each species that appeared within each census plot. The abundances of sessile and mobile organisms in each census plot just after summer (October or November) from 2004 to 2018 were used to calculate the total abundances summed over all plots at all shores for each species in each year.

Data analysis

To evaluate the impact of MHWs on community abundance and the abundance of each species at the regional scale, I calculated the total abundance over all plots for each species in each year. I used the data for the total abundance of all plots because the thermal environment is expected to have large spatial variation within the range encompassing the metapopulation scale of marine benthos (Helmuth et al. 2002, 2006). Because the differences in the number of plots at each shore was small (all shores had 4 or 5 plots), I ignored any differences in abundance between shores and used the same method to obtain the total abundance at the regional scale. I believe that this had little effect on the estimation of regional abundance.

When assessing the effect of MHWs on the abundance of individual species, I selected common species that occurred in more than seven records in surveys during the 15 years. The data for rare species that were recorded only a few times in the 15-year period could contain large observational errors, making it difficult to accurately estimate abundance and the traits of species' niches. In the case of the invasive barnacle *Balanus glandula*, whose introduction to the study area occurred relatively recently, the population dynamics may not have reached equilibrium (Noda and Ohira. 2020), making it difficult to precisely assess the effects of MHWs on their population dynamics. They were therefore excluded from the analysis. On the basis of the above criteria, 25 rocky intertidal macro-benthic species were included in analysis of the effects of MHWs at the species level: 12 algae, 5 sessile invertebrates, 6 herbivorous mollusks, and 2 carnivorous invertebrates (Table 3-1).

Estimation of effect sizes

To evaluate the effects of MHWs on each functional group and each species, I calculated the effect sizes (Iwasaki et al. 2016; Noda et al. 2017; Iwasaki and Noda. 2018) of the abundance of each functional group and each species from before the MHWs (2004–2009) to during (2010–2016) and after (2017 and 2018) using the following formulas:

$$\boldsymbol{Effect\ size\ of\ each\ functional\ group} = \frac{\boldsymbol{F_{during-after} - \overline{F}_{before}}}{\boldsymbol{SD(F_{before})}}$$

$$\boldsymbol{Effect\ size\ of\ each\ species} = \frac{\boldsymbol{(S_{during-after} + 0.5) - \overline{S}_{before}}}{\boldsymbol{SD(S_{before})}}$$

where $F_{\text{during-after}}$ represents sum of the $\log_{10}$(abundance) of each functional group for each year during or after the MHWs. $\bar{F}_{\text{before}}$ and SD(F_{before}) are the mean and standard deviation, respectively, for the sum of $\log_{10}$(abundance) of each functional group for each year before the MHWs. $S_{\text{during-after}}$ represents the sum of $\log_{10}$(abundance) of each species for each year during or after the MHWs. $\bar{S}_{\text{before}}$ and SD(S_{before}) are the mean and standard deviation, respectively, for the sum of $\log_{10}$(abundance + 0.5) of each species for each year before the MHWs.

Species niche traits

I estimated the thermal niche for all species as a species niche trait. I also estimated the vertical niche for sessile species.

Thermal niches

The position of the thermal niche (i.e., the preferred temperature) for each species was estimated from information on sea surface temperatures in the ecoregion in which each species was distributed (Spalding et al. 2007) using the following formula:

$$\boldsymbol{Thermal\ niches} = \frac{(\boldsymbol{SSTs\ of\ northern\ range\ limit + SSTs\ of\ southern\ range\ limit})}{\mathbf{2}}$$

where SSTs are mean annual sea surface temperatures. The mean annual sea surface temperatures for each ecoregion corresponding to the northern and southern range limits were obtained from Payne et al. (2012).

An ecoregion is part of a biogeographic schema, that is, a global hierarchical classification system based on marine coastal environments (Spalding et al. 2007). The biogeographic schema is a nested system of 12 realms, 62 provinces and 232 ecoregions (Spalding et al.2007). My study area is included within the Oyashio Current ecoregion within the temperate northern Pacific realm. In previous studies, thermal niches were estimated by defining northern (i.e., cold-affinity) species and southern (i.e., warmer-water) species using species occurrence reports (Smale et al. 2017; Sanford et al. 2019). Thus, I obtained occurrence reports for each species from Hayashi (1943, 1947), Toyokokujigyo Corporation. (1980), Pasco Corporation. (1988), Korn and Kulikova (1995), Yoshida (1998), Higo et al. (1999), Okutani (2000), Selivanova (2002), Kado (2003), Latypov and Kasyanov (2003), Nishi (2003), Okuda et al. (2010), Yamazaki (2011), Fukui and Kashiwao (2012), Cox et al. (2014), Kanamori et al. (2017), Association for the Research of Littoral Organisms in Osaka Bay (2018), Hanyuda et al. (2018), Ito et al. (2018, 2019), Marko and Zaslavskaya (2019), Klochkova et al. (2020, 2021), Noda and Ohira (2020), and Ishida et al. (2021). Here, I focused on the distribution of each species in four ecoregions along the coastal northwest Pacific within the temperate northern Pacific realm: Kamchatka Shelf and Coast, Oyashio Current, Northeastern Honshu, and Central Kuroshio Current. These four ecoregions with their distinct latitudinal gradients in sea surface temperatures (Payne et al. 2012) are suitable as indicators of biogeographic affinity for each species. For example, for species distributed in the Gulf of Alaska (51.0–64.8°N) and the Oyashio Current (39.6–52.8°N), the northern limit would be the Gulf of Alaska, but the mean annual surface seawater temperature in this ecoregion is higher than that in the Oyashio Current (Payne et al. 2012); this is contrary to the "expected" latitudinal gradient of the colder north and the warmer south. In addition, using these four ecoregions for defining ranges reflects the natural distribution of the area. For example, *Ulva pertusa*, which is distributed in tropical regions, may have been introduced from temperate regions as a non-indigenous species (Hanyuda et al. 2016). The number of reported occurrences of individual species was well described within these four ecoregions, and the occurrence reports in four ecoregions of many species were similar, so I can accurately determine cold-affinity species and warmer-water species.

Vertical niches

For each of the 17 sessile species, the mode of zonation was estimated as a measure of their vertical niche position. First, I estimated the vertical profile of the distribution of each species over the entire vertical extent of the intertidal zone. For this, in May 2017 I extended each survey plot in the 2004–2018 survey by 50 cm vertically above and below the original plot, placed 400 grid points at 5-cm intervals both vertically and horizontally on the rock surface within each extended survey plot as in the 2004–2018 survey, and recorded the species of sessile organisms occupying each grid point. The elevation of each grid point was estimated by using the slope of the rock walls measured at 25-cm vertical intervals on each rock. Thus, I obtained data for the occupancy within each 200 cm high by 50 cm wide census plot (400 grid points) in May 2017, data for the occupancy within each 100 cm high by 50 cm wide census plot (200 grid points) obtained from the surveys conducted in autumn from 2004 to 2018, and an estimated elevation for each grid point. From these data, I determined the mean abundance of each sessile species in the each of 20 elevation classes (100–90 cm, 90–80 cm ... –80 to –90 cm, and –90 to –100 cm from mean tidal level), corresponding to the rock surface in each census plot divided into 10-cm elevation intervals. The vertical niche of each sessile species was calculated from the average abundance of all elevation classes obtained using the following formula:

$$\boldsymbol{Vertical\,niches} = \frac{\sum_{H=1}^{20} \boldsymbol{H} \times \boldsymbol{S_{S,H}}}{\sum_{H=1}^{20} \boldsymbol{S_{S,H}}}$$

where H is the elevation class defined as 1 at –90 to –100 cm from mean tidal level. $S_{\mathrm{S,H}}$ represents the frequency of occurrence of species S in elevation class H. Values of vertical niches are larger in species that inhabit higher elevations.

Statistical analysis

If there are accumulative carryover effects from MHWs on population and community dynamics, then the difference in abundance during MHWs and under normal conditions should be small immediately after the MHW, but then increase with the elapsed time from the MHW event. Therefore, to detect whether there was a temporal trend in the changes in the community abundance of the four functional groups or the abundance of each species during the MHWs, I conducted linear regression analysis, with the number of years (1–7) since the onset of the MHWs as the explanatory variable and the effect sizes of the abundances of four functional groups and 25 species from 2010 to 2016 as response variables. Here, a significant slope and a non-significant intercept were considered evidence of accumulative carryover effects.

To determine whether ignoring accumulative carryover effects would result in a biased assessment of the effects of MHWs on the abundance of each functional group and each species during the MHWs and for two years after they ended (when sea surface temperatures returned to normal), I calculated both the average effect sizes from 2010–2016 and the accumulative carryover effect sizes. For the latter measure, I used the effect size in the last year of the MHWs (2016) for species for which an accumulative carryover effect was detected, and the average effect size from 2010 to 2016 for species for which no accumulative carryover effect was found.

I examined how the effects of MHWs on the abundance of each species of sessile organisms (macroalgae and sessile invertebrates) differed following during the onset of the MHWs (2010–2016) and during the first year (2017) and the second year (2018) after the MHWs, depending on species niche traits (thermal and vertical niches). I performed multiple regression analysis in which the effect size of the abundance of sessile species from 2010–2016, 2017, and 2018, or consideration of the accumulative carryover effect, were treated as response variables, and the species niche traits (standardized thermal niches and standardized vertical niches) were explanatory variables. The two functional groups of sessile species were combined because the number of sessile invertebrate species (5 species) was much smaller than that of macroalgae (12 species).

I examined how the effects of MHWs on the abundance of each species of mobile organism (herbivorous mollusks and carnivorous invertebrates) differed following during the onset (2010–2016) and during the first (2017) and second year (2018) after the MHWs, depending on thermal niche. I performed linear regression analysis, in which the effect size of the abundance of mobile species from 2010–2016, 2017, and 2018, or consideration of the accumulative carryover effects were treated as response variables, and the standardized thermal niches were explanatory variables. The two functional groups were combined as mobile species because the number of species of carnivorous invertebrates was low (2 species) compared to herbivorous mollusks (6 species). All linear and multiple regressions were performed after checking the data for normality by using the Shapiro-Wilk test. All statistical analyses were executed using R version 4.1.2.

3.3. Results

Accumulative carryover effects

The accumulative carryover effects of the MHWs on community abundance at the regional scale varied among four functional groups of rocky intertidal organisms. There was a positive carryover effect for macroalgae and a negative one for carnivorous invertebrates (Table 3-2), whereas there were no apparent accumulative carryover effects for sessile invertebrates or herbivorous mollusks.

The accumulative carryover effects of the MHWs on regional population size varied among functional groups. Accumulative carryover effects were detected for 6 out of the 25 species (24%); i.e., these species increased or decreased in abundance with the number of years after the onset of the MHWs (Table 3-1). Negative accumulative carryover effects were detected for 2 out of 12 species of macroalgae (16.7%) and one of the two species of carnivorous invertebrates, whereas a positive accumulative carryover effect was detected for one out of six species of herbivorous mollusks (2%). In contrast, no accumulative carryover effects were detected for sessile invertebrate species.

Effect size of community abundance for each functional group during and after MHWs

The effect of the MHWs on community abundance at the regional scale varied among the four functional groups of the rocky intertidal community. There were significant positive effects on macroalgae during the MHWs (2010–2016), in the last year of the MHWs, and in the first and second years after the MHWs (Fig. 3-3). The MHWs did not have any significant impact on sessile invertebrates. MHWs had significant negative effects on herbivorous mollusks during the MHWs (2010–2016), and in the first and second years after the MHWs (Fig. 3-3). MHWs had significant negative effects on carnivorous invertebrates during the MHWs, in the last year of the MHWs, and in the first year after the MHWs.

Effect size of abundance of each species during and after MHWs

The effect of the MHWs on regional population size varied among functional groups. For macroalgae, MHWs had significant positive effects on 50% of the species during the MHWs (50.0%), whereas there were no significant effects on the majority of species in 2017 and 2018 (both 66.7%) (Fig. 3-4). MHWs had a significant positive effect on *Corallina pilulifera* and *Hildenbrandia* spp. during the MHWs (2010–2016), and in the first and second years after the MHWs. MHWs had positive effects on the majority of species of macroalgae during the MHWs (2010–2016), and in the first and the second year after the MHWs. The effects of the MHWs on regional population size in the last year of the MHWs differed between two species for which there were negative accumulative carryover effects: the population size of *Pterosiphonia bipinnata* decreased significantly, but that of *Cladophora opaca* did not.

For sessile invertebrates, most species (80–100%) were unaffected by MHWs during the MHWs (2010–2016), or in the first or second years after the MHWs.

For herbivorous mollusks, MHWs had significant negative effects on 50% or more of the species during the MHWs (50.0%), and in the first and second years after the MHWs (66.7% and 50.0%, respectively). The MHWs had a significant negative impact on *Littorina sitkana* and *Stenotis uchidai* during the MHWs (2010–2016), and in the first and second years after the MHWs. MHWs had negative effects on the majority of species of herbivorous mollusks during the MHWs (2010–2016), and in the first and second years after the MHWs. MHWs had a positive effect on *Littorina brevicula* in the last year of the MHWs, and in the first and second years after the MHWs, in which positive accumulative carryover effects were detected. MHWs had a significant negative impact in the last year of the MHWs for both species for which negative accumulative carryover effects were found.

For the two carnivorous invertebrate species, MHWs had significant negative effects on both during the MHWs (2010–2016) and in the first year after the MHWs. The MHWs also had a significant negative impact on *Leptasterias ochotensis similispinis* during the second year after the MHWs. MHWs had a significant negative impact in the last year of the MHWs for *Nucella lima*, for which there were also negative accumulative carryover effects.

Effects of MHWs by species niches traits

The results of multiple regression analysis for sessile organisms showed significant effects only for thermal niches, regardless of the response variables. That is, the MHWs caused changes in composition of sessile assemblages at a regional scale by reducing the abundances of species with low thermal niches (i.e., cold-affinity species) and increasing those of species with high thermal niches (i.e., warmer-water species) (Table 3-3 and Fig. 3-5).

The results of linear regression analysis for mobile organisms showed significant effects for thermal niches regardless of the response variables. That is, the MHWs caused changes in the composition of mobile assemblages at a regional scale by reducing the abundances of species with low thermal niches (i.e., cold-affinity species) and increasing those of species with high thermal niches (i.e., warmer-water species) (Table 3-4 and Fig. 3-5).

This result indicates the increase in abundance due to MHWs in warmer-water species is more pronounced for species with higher vertical niches. The results of multiple regression analysis for each species of sessile organisms when considering accumulative carryover effects showed a significant interaction between thermal and vertical niches (Table 3-5). This indicates that the increase in abundance due to MHWs in warmer-water species is more pronounced for species with higher vertical niches.

The results of linear regression analysis for each species of mobile animal when considering the accumulative carryover effects showed no effect by thermal niche (Table 3-6).

3.4. Discussion

In this study, I evaluated the impacts of the MHWs in southeastern Hokkaido in summer (July–September) from 2010 to 2016 on the abundances and by species niche traits of rocky intertidal communities (macroalgae, sessile invertebrates, herbivorous mollusks and carnivorous invertebrates) by separating the effects of MHWs from those of other environmental stochasticity. I found positive and negative accumulative carryover effects of MHWs (i.e., a continued increase or decrease in abundance with the number of years elapsed since the onset of the MHWs) in the community abundance of macroalgae and carnivorous invertebrates, respectively (Table 3-2). At the species level, accumulative carryover effects were detected in 6 out of 25 species (Table 3-1). In addition, I found differences in the response to MHWs in terms of community abundance among four functional groups. Macroalgae increased during and after the MHWs, whereas sessile invertebrates showed no response (Fig. 3-3). Herbivorous mollusks decreased in abundance during and after the MHWs. Carnivorous invertebrates decreased in abundance during the MHWs and in the first year afterward. Finally, we found reduced abundances of species with low thermal niches (i.e., cold-affinity species) and increased abundances of those with high thermal niches (i.e., warmer-water species) (Table 3-3 and 3-4 and Fig. 3-5). The increase in abundance of warmer-water species due to MHWs is more pronounced for species with higher vertical niches, but this became evident only when accumulative carryover effects were considered (Tables 3-3 and 3-5).

Accumulative carryover effects

The frequency of MHWs has increased in recent years (Hobday et al. 2018; Oliver et al. 2018). Therefore, it is important to clarify whether MHWs have an accumulative carryover effect when they occur continuously or persist over multiple years. In this study, accumulative carryover effects caused by consecutive MHWs were detected in both the community abundance of functional groups and the abundance of individual species. The interpretation of the impact of MHWs on the community abundance of functional groups was the same with or without consideration of accumulative carryover effects, with a significant increase in macroalgae and a significant decrease in carnivorous invertebrates (Fig. 3-3). In contrast, the interpretation of the impact of MHWs on the abundance of individual species for which accumulative carryover effects were found differed when those effects were considered. There were no significant effects during the MHWs, but for the effect size calculated considering accumulative carryover effects two of the six species (*Pterosiphonia bipinnata* in macroalgae and *Lottia cassis* in herbivorous mollusks) showed a significant decrease and one species (*Littorina brevicula* in herbivorous mollusks) showed a significant increase (Fig. 3-4). These results emphasize that the response of organisms to MHWs should be evaluated even when accumulative carryover effects are considered.

The 5 species out of 25 for which negative accumulative carryover effects were found included four species for which significant negative effects were detected in the last year of the MHWs (2016)—the macroalga *Pterosiphonia bipinnata*, herbivorous mollusks *Lottia cassis* and *Stenotis uchidai*, and the predatory invertebrate *Nucella lima*—as well as one species for which no MHW effects were detected in 2016: the macroalga *Cladophora opaca* (Fig. 3-4). This suggests that these five species are particularly susceptible when MHWs occur continuously or persist for a period of time. In *Cladophora opaca*, the mechanism by which negative accumulative carryover effects were observed but without significant negative effects in 2016 is unknown, but perhaps this species had a higher thermal niche (Table 3-7) than the other four species for which negative accumulative carryover effects were found, and it was not affected in 2016 because it is less sensitive to MHWs.

My results show that sequential MHWs caused an accumulative carryover effect on marine community abundance and population size. In some species, the effects of the MHWs could be underestimated if the accumulative carryover effects were not considered. However, there are still outstanding questions regarding the accumulative carryover effects of MHWs on marine organisms. First, it is not clear how the tendency to cause accumulative carryover effects depends on species niche traits. For example, species with longer life histories and smaller dispersal ability are more likely to show accumulative carryover effects on population size when sequential MHWs occur. Unfortunately, I was unable to test this hypothesis in this study because there were fewer annual and non-planktonic species (7 and 4 species, respectively) than perennial and planktonic species. Second, it is not clear which functional groups and species niche traits of the organisms affected are particularly susceptible to the accumulative carryover effects of MHWs. In this study, four of the five species for which negative accumulative carryover effects were found (Table 3-1) had significant negative effects detected in the last year of the MHWs (2016), whereas one species showed no significant negative effects in 2016 (Fig. 3-4). This suggests that there are functional groups or species niche traits that are particularly susceptible among those that show accumulative carryover effects. However, this hypothesis could not be tested in this study because of the small number of species showing an accumulative carryover effect.

Effect size of community abundance for each functional group during and after MHWs

The response of rocky intertidal communities to MHWs has been mainly investigated for relatively strong MHWs (categories I–III) (Hobday et al. 2018) in the northeast Pacific (Sanford et al. 2019; Miner et al. 2021; Suryan et al. 2021; Weitzman et al. 2021; Spiecker and Menge. 2022). Little is known, therefore, about how relatively weak MHWs (categories I and II) affect rocky intertidal communities. I examined the effects of category I and II MHWs (Miyama et al. 2021a, b) that occur every summer (July–September) at my study site, thus filling this gap in our knowledge. Despite the relatively weak category I or II MHWs that occurred in southeastern Hokkaido, Japan, from 2010 to 2016, there were few signs of community abundance recovery in the major functional groups by the second year after the MHWs. Of the functional groups that increased or decreased in abundance during and after MHWs (macroalgae, herbivorous mollusks and carnivorous invertebrates), both macroalgae and herbivorous mollusks remained higher and lower in abundance, respectively, in the second year after the MHWs (2018) (Fig. 3-3).

There are two possible reasons for the increase in macroalgal community abundance during the MHWs in southeastern Hokkaido. First, the increase in overall abundance of macroalgae may have been caused by an increase in warmer-water species due to the increase in sea surface temperatures caused by MHWs. This is because the species that comprise the macroalgae are relatively dominated by warmer-water species with thermal niches greater than 10 (Table 3-7). Four of these species, which include the dominant crustose coralline algae *Corallina pilulifera* and the red alga *Gloiopeltis furcata* (Kanamori et al. 2017; Ishida et al. 2021), showed increases in both the mean effect size during the MHWs, and in the effect size in the first and second years after the MHWs (Fig. 3-4). Second, the increase in community abundance of macroalgae may have been caused by a trophic cascade resulting from a decline in herbivorous invertebrate abundance due to MHWs. This is supported by the fact that the abundance of algal communities in rocky intertidal zones is restricted by grazing pressure (Cubit. 1984; Guerry et al. 2009; Poore et al. 2012). The community abundances of herbivorous mollusks and carnivorous invertebrates showed a negative response to MHWs (Fig. 3-3). Compared to macroalgae and sessile invertebrates, many species of herbivorous mollusks and carnivorous invertebrates have lower thermal niches (Table 3-7); also, the higher trophic levels are regulated by environmental stress (Menge and Sutherland. 1987; Menge and Olson. 1990), which may have caused a decline in community abundance. These results are likely due to MHWs, as there was no linear increasing or decreasing trend in the group abundance of the four functional groups in 2004-2009, before the onset of MHWs (Table S3-1).

My results show a significant positive effect of MHWs for the community abundance of macroalgae in all periods (during and after the MHWs), whereas MHWs had no effect on the community abundance of sessile invertebrates in any period (Fig. 3-3). In contrast, previous studies showed a decrease in algae after the 2014–2016 northeast Pacific MHW in the Gulf of Alaska, but an increase in sessile animals (Suryan et al. 2021; Weitzman et al. 2021). Despite being in the same ecosystem (i.e., rocky intertidal zones), there are a variety of factors that might have caused the differences in responses between this study and those in the Northeast Pacific region. There were differences in MHW intensity (categories I and II, Miyama et al. 2021a, b vs. categories I–III, Hobday et al. 2018), species composition (*Fucus* and mussels are not dominant species in my study area; Kanamori et al. 2017; Ishida et al. 2021) and in thermal niches of the component species. More reports on the responses of marine organisms to MHWs are needed for various ecosystems, regions, and organisms, including information on the intensity of MHWs, in order to identify factors that result in differences in responses to MHWs in the same ecosystem. Identification of these factors would facilitate our understanding of the areas and functional groups that are susceptible to MHWs and would thus help in the conservation of marine ecosystems.

Quantifying community abundance responses to MHWs in southeastern Hokkaido, Japan, from 2010-2016 by effect size revealed that community abundance of macroalgae increased both during MHWs and in the first and second year after MHWs, community abundance of herbivorous mollusks decreased both during MHWs and in the first and second year after MHWs, and community abundance of carnivorous invertebrates decreased both during MHWs and in the first year after MHWs (Fig. 3-3). When quantified by changes in community abundance, macroalgae increased 1.271, 1.278, and 1.389 times during MHWs and in 2017 and 2018, respectively, compared to the average abundance before the MHWs events (Table S3-2). The abundance of herbivorous mollusks decreased by a fold of 1.310, 2.017, and 1.712 during MHWs, 2017, and 2018, respectively, compared to the mean abundance before the MHWs (Table S3-2). The abundance of carnivorous invertebrates declined by a fold of 2.472 and 15.731 during MHWs and in 2017, respectively, compared to the mean abundance before the MHWs (Table S3-2). Since most of the previous studies have evaluated the effects of ocean heat waves based on comparisons of abundance obtained from surveys before and after MHW events (Smale and Wernberg. 2013; Wernberg et al. 2013; Smale et al. 2017; Sanford et al. 2019; Thomsen et al. 2019; Weitzman et al. 2021), mentioning changes in abundance may provide useful information for future meta-analysis of the response of marine organisms to MHWs in terms of the amount of change in abundance.

Effects of MHWs by species niches traits

Identifying the species niche traits susceptible to MHWs will improve the predictability the responses of marine organisms to MHWs. My results show that the abundances of species with low thermal niches decreased during and after MHWs, whereas those of species with high thermal niches increased (Tables 3-3 and 3-4 and Fig. 3-5). Previous studies have suggested a decrease in abundance of cold-affinity species (Smale et al. 2017) and an increase in warmer-water species (Smale et al. 2017; Sanford et al. 2019; Miner et al. 2021). These studies suggest that focusing on thermal niches can be useful for understanding and predicting the ecological processes behind the responses of marine organisms to MHWs. When I considered accumulative carryover effects for mobile animals, there were no differences in the response to MHWs by thermal niche (Table 3-6), possibly because the abundance of *Lottia cassis*, which has a relatively high thermal niche among mobile animals (Table 3-7), was drastically reduced by accumulative carryover effects (Fig. 3-4).

My examination of the effects of thermal and vertical niches on species-specific responses to MHWs did not support my prediction that sessile rocky intertidal species with higher vertical distributions (i.e., higher vertical niches) would likely be less affected by MHWs. One possible reason why my prediction was not supported by my results is that the MHWs might affect regional-scale population sizes of rocky intertidal sessile species through complex mechanisms, including direct and indirect effects of changes in seawater temperature, which to date have been rarely examined in empirical studies. To deepen my understanding of the influence of MHWs on rocky intertidal communities, studies focusing on the underlying mechanisms that cause interspecific differences in MHW responses are eagerly awaited. As a cause of interspecific differences in responses to MHWs, both this and previous studies emphasize the importance of thermal niches. However, the influence and importance of vertical niches are still unknown. Although the present study demonstrates that the increase in abundance of warmer-water species due to MHWs is more pronounced for species with higher vertical niches, a previous study suggested that vertical niches may not be an important factor for explaining interspecific differences in response to MHWs; in the Northeast Pacific, changes in the percent cover of each rocky intertidal taxon during and after marine heat waves were similar in both the middle and lower strata of the intertidal zone (Weitzman et al. 2021).

3.5. Conclusions

In this study, I examined the response of rocky intertidal communities to relatively weak (categories I and II) MHWs that occurred southeast of Hokkaido, northern Japan, in summer (July–September) from 2010 to 2016. The specific questions addressed were (1) Did MHWs have an accumulative carryover effect on the community abundance of the four main functional groups or on the abundance of each species? (2) How did the effects of MHWs on the community abundance of the four functional groups during the MHWs (2010–2016) and subsequent recovery in the first (2017) and second (2018) years after the MHWs differ? (3) How did the susceptibility to MHWs differ depending on two species niche traits, i.e., thermal and vertical niches?

I found that (1) the continuous MHWs had an accumulative carryover effect on both functional group abundance and the abundance of individual species. In addition, some species for which accumulative carryover effects were detected were underestimated when those effects were not considered.

(2) The community abundance of macroalgae and herbivorous mollusks increased and decreased, respectively, during the MHWs (2010–2016), and in the first and second years after the MHWs, and the community abundance of carnivorous invertebrates decreased during the MHWs and in the first year after. The increase in community abundance of macroalgae may have occurred because the macroalgal communities are composed of a relatively large number of warmer-water species, and/or by a trophic cascade resulting from a decrease in herbivorous invertebrates. The decline in community abundance of herbivorous mollusks and carnivorous invertebrates may have been caused by the fact

that these communities are composed of a relatively large number of species with more cold-affinity.

(3) The abundance of species distributed in colder water (i.e., lower thermal niches) decreased and those distributed in warmer water (i.e., higher thermal niches) increased. There were no detectable differences in response to MHWs between species distributed at higher vertical positions (i.e., higher vertical niches) and those at lower vertical positions (i.e., lower vertical niches) when accumulative carryover effects were not considered. On the other hand, the increase in abundance due to MHWs in warmer-water species is more pronounced for species with higher vertical niches when accumulative carryover effects are considered.

The results of this study agree with those of a previous study conducted on subtidal communities (Smale et al. 2017) in that the susceptibility to MHWs is related to the thermal niche traits of the species. On the other hand, for the response of functional groups to MHWs, my results are not consistent with those of previous study (Weitzman et al.2021), despite being in the same intertidal ecosystem (i.e., rocky intertidal). Thus the findings from studies to date are insufficient to predict the effects of MHWs on marine ecosystems, and further studies are needed to elucidate the response of marine organisms to MHW events of various intensities and durations for a variety of ecosystems, regions, and organisms.

References

Association for the Research of Littoral Organisms in Osaka Bay. 2018. Rocky shore macrobiota of southeastern Osaka Bay: Results of surveys carried out in the years 2011-2015. Occasional papers from the Osaka Museum of Natural History 4:17-40. (in Japanese with English abstract).

Benedetti-Cecchi, L., I. Bertocci, S. Vaselli, and E. Maggi. 2006. Temporal variance reverses the impact of high mean intensity of stress in climate change experiments. Ecology 87:2489–2499.

Cubit, J. D. 1984. Herbivory and the seasonal abundance of algae on a high intertidal rocky shore. Ecology 65:1904–1917.

Frölicher, T. L., E. M. Fischer, and N. Gruber. 2018. Marine heatwaves under global warming. Nature 560:360–364.

Fukui, S., and S. Kashiwao. 2012. Molluscan Fauna of Usujiri Marine Station Field Science Center for Northern Biosphere, Hokkaido University: Second Edition. Hokkaido University.(in Japanese).

Guerry, A. D., B. A. Menge, and R. A. Dunmore. 2009. Effects of consumers and enrichment on abundance and diversity of benthic algae in a rocky intertidal community. Journal of Experimental Marine Biology and Ecology 369:155–164.

Hanyuda, T., G. I. Hansen, and H. Kawai. 2018. Genetic identification of macroalgal species on Japanese tsunami marine debris and genetic comparisons with their wild populations. Marine Pollution Bulletin 132:74–81.

Hanyuda, T., S. Heesch, W. Nelson, J. Sutherland, S. Arai, S. M. Boo, and H. Kawai. 2016. Genetic diversity and biogeography of native and introduced populations of Ulva pertusa (Ulvales, Chlorophyta). Phycological Research 64:102–109.

Hayashi, R.1943. Contributions to the Classification of the Sea-stars of Japan. II. Forcipulata, with the Note on the Relationships between the Skeletal Structure and Respiratory Organs of the Sea-stars. Journal of the Faculty of Science, Hokkaido University. Series 6, Zoology 8: 133–281.

Hayashi, R.1947. The Fauna of Akkeshi Bay: XVI. Asteroidea. Journal of the Faculty of Science, Hokkaido University. Series 6, Zoology 9: 277-280.

Helmuth, B., C. D. G. Harley, P. M. Halpin, M. O'Donnell, G. E. Hofmann, and C. A. Blanchette. 2002. Climate change and latitudinal patterns of intertidal thermal stress. Science 298:1015–1017.

Helmuth, B., N. Mieszkowska, P. Moore, and S. J. Hawkins. 2006. Living on the edge of two changing worlds: Forecasting the responses of rocky intertidal ecosystems to climate change. Annual Review of Ecology, Evolution, and Systematics 37:373–404.

Higo, S,. P. Callomon, and Y. Goto. 1999. Catalogue and bibliography of the marine shell-bearing mollusca of Japan : gastropoda, bivalvia, polyplacophora, scaphopoda.Elle Scientific Publications, Yao.

Hobday, A. J., L. V. Alexander, S. E. Perkins, D. A. Smale, S. C. Straub, E. C. J. Oliver, J. A. Benthuysen, M. T. Burrows, M. G. Donat, M. Feng, N. J. Holbrook, P. J. Moore, H. A. Scannell, A. Sen Gupta, and T. Wernberg. 2016. A hierarchical approach to defining marine heatwaves. Progress in Oceanography 141:227–238.

Hobday, A. J., E. C. Oliver, A. S. Gupta, J. A. Benthuysen, M. T. Burrows, M. G. Donat, N. J. Holbrook, P. J. Moore, M. S. Thomsen, T. Wernberg and D. A. Smale. 2018. Categorizing and naming marine heatwaves. Oceanography 31: 162–173.

Ishida, K., M. Tachibana, M. Hori, T. Okuda, T. Yamamoto, M. Nakaoka, and T. Noda. 2021. Quantifying the dynamics of rocky intertidal sessile communities along the Pacific coast of Japan: implications for ecological resilience. Scientific Reports 11:1–12.

Itoh, T., I.Ueda., K. Hagiwara., M. Kitajima., T. Iwasaki., K. Muraishi., and T. Sakiyama. 2018. Intertidal animals found on Enoshima Island – VII. Natural

History Report of Kanagawa 39: 13–21. (in Japanese with English abstract).

Itoh, T., M. Miyadai., and A. Kobayashi. 2019. Marine algal flora in the intertidal and shallow infralittoral zones of Enoshima Island, Sagami Bay, Japan. Natural History Report of Kanagawa 40: 5–14. (in Japanese with English abstract).

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

Iwasaki, A., and T. Noda. 2018. A framework for quantifying the relationship between intensity and severity of impact of disturbance across types of events and species. Scientific Reports 8:1–7.

Iwataki, M., W. M. Lum, K. Kuwata, K. Takahashi, D. Arima, T. Kuribayashi, Y. Kosaka, N. Hasegawa, T. Watanabe, T. Shikata, T. Isada, T. Y. Orlova, and S. Sakamoto. 2022. Morphological variation and phylogeny of Karenia selliformis (Gymnodiniales, Dinophyceae) in an intensive cold-water algal bloom in eastern Hokkaido, Japan. Harmful Algae 114:102204.

Kado, R. 2003. Invasion of Japanese shores by the NE Pacific barnacle Balanus glandula and its ecological and biogeographical impact. Marine Ecology Progress Series 249:199–206.

Kanamori, Y., K. Fukaya, and T. Noda. 2017. Seasonal changes in community structure along a vertical gradient: patterns and processes in rocky intertidal sessile assemblages. Population Ecology 59:301–313.

Klochkova, N. G., T. A. Klochkova, and A. V. Klimova. 2020. Marine Benthic Algae From Commander Islands (Revision 2020). I. Chlorophyta and Ochrophyta. Bulletin of Kamchatka State Technical University:82–107. (in Russian with

English abstract).

Klochkova, N. G., T. A. Klochkova, and A. V. Klimova. 2021. Marine Benthic Algae From Commander Islands (Revision 2021). II. Rhodophyta. Bulletin of Kamchatka State Technical University:41–72. (in Russian with English abstract).

Korn, O. M., and V. A. Kulikova. 1995. Seasonal species composition and distribution of barnacle larvae in Avacha Inlet (Kamchatka). Journal of Plankton Research 17:221–234.

Latypov, Y. Y., and V. L. Kasyanov. 2003. Biodiversity of the Commander Islands and Bering Sea Coast of the Kamchatka Peninsula by Russian Scientists. In Proceedings of the Arctic Biodiversity Workshop: new census of marine life initiative (eds. Iken, K., and B. Konar). Alaska Sea Grant College Program University of Alaska Fairbanks, pp. 59‒66.

Marko, P. B., and N. I. Zaslavskaya. 2019. Geographic origin and timing of colonization of the Pacific Coast of North America by the rocky shore gastropod Littorina sitkana. PeerJ 2019:1–26.

Menge, B. A., and A. M. Olson. 1990. Role of scale and environmental factors in regulation of community structure. Trends in Ecology and Evolution 5:52–57.

Menge, B. A., and J. P. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. American Naturalist 130:730–757.

Miner, C. M., J. L. Burnaford, K. Ammann, B. H. Becker, S. C. Fradkin, S. Ostermann-Kelm, J. R. Smith, S. G. Whitaker, and P. T. Raimondi. 2021. Latitudinal variation in long-term stability of North American rocky intertidal communities. Journal of Animal Ecology 90:2077–2093.

Misaka, T., and Y. Ando. 2021. Large-scale outbreak of Harmful Algae in the Pacific Coast of Hokkaido, Japan.

https://www.hro.or.jp/list/fisheries/marine/att/ima943.pdf. (in Japanese).

Miyama, T., S. Minobe, and H. Goto. 2021a. Marine Heatwave of Sea Surface Temperature of the Oyashio Region in Summer in 2010–2016. Frontiers in Marine Science 7:1–13.

Miyama, T., S. Minobe, and H. Goto. 2021b. Frequent Marine Heat Waves Off the Coast of Hokkaido and Tohoku Revealed: Relationship between Marine Heat Waves and Yellowtail Catches. https://www.hokudai.ac.jp/news/pdf/210114_pr4.pdf. (in Japanese).

Nicole Cox, L., N. I. Zaslavskaya, and P. B. Marko. 2014. Phylogeography and trans-Pacific divergence of the rocky shore gastropod Nucella lima. Journal of Biogeography 41:615–627.

Nishi, E. 2003. Polychaetes (annelids, polychaetes) from the waters around Manazuru Peninsula, Sagami Bay, Japan. Actinia : bulletin of the Manazuru Marine Laboratory for Science Education, Faculty of Education and Human Sciences, Yokohama National University 15: 7–13. (in Japanese with English abstract).

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

Noda, T. 2009. Metacommunity-level coexistence mechanisms in rocky intertidal sessile assemblages based on a new empirical synthesis. Population Ecology 51: 41-55.

Noda, T., and M. Ohira. 2020. Transition in population dynamics of the intertidal barnacle balanus glandula after invasion: Causes and consequences of change in larval supply. Journal of Marine Science and Engineering 8:1–10.

Noda, T., M. Sakaguchi, A. Iwasaki, and K. Fukaya. 2017. Influence of the 2011 Tohoku Earthquake on population dynamics of a rocky intertidal barnacle: cause and consequence of alteration in larval recruitment. Coastal marine science 40:35–43.

Okuda, T., T. Noda, T. Yamamoto, M. Hori, and M. Nakaoka. 2010. Contribution of environmental and spatial processes to rocky intertidal metacommunity structure. Acta Oecologica 36:413–422.

Okutani, T. 2000. Marine mollusks in japan. Tokai University press, Tokyo.(in Japanese).

Oliver, E. C. J., M. G. Donat, M. T. Burrows, P. J. Moore, D. A. Smale, L. V. Alexander, J. A. Benthuysen, M. Feng, A. Sen Gupta, A. J. Hobday, N. J. Holbrook, S. E. Perkins-Kirkpatrick, H. A. Scannell, S. C. Straub, and T. Wernberg. 2018. Longer and more frequent marine heatwaves over the past century. Nature Communications 9:1–12.

Pasco Corporation.1988. Third Basic Survey for Conservation of the Natural Environment Marine Area Survey Report of Marine Biological Environment Survey (All parts of Japan Version). (in Japanese).

Payne, M. C., C. A. Brown, D. A. Reusser, and H. Lee. 2012. Ecoregional analysis of nearshore sea-surface temperature in the North Pacific. PLoS ONE 7: e30105.

Poore, A. G. B., A. H. Campbell, R. A. Coleman, G. J. Edgar, V. Jormalainen, P. L. Reynolds, E. E. Sotka, J. J. Stachowicz, R. B. Taylor, M. A. Vanderklift, and J. Emmett Duffy. 2012. Global patterns in the impact of marine herbivores on benthic primary producers. Ecology Letters 15:912–922.

R Core Team. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/ (2021).

Ruthrof, K. X., D. D. Breshears, J. B. Fontaine, R. H. Froend, G. Matusick, J. Kala, B. P. Miller, P. J. Mitchell, S. K. Wilson, M. van Keulen, N. J. Enright, D. J. Law, T.

Wernberg, and G. E. S. J. Hardy. 2018. Subcontinental heat wave triggers terrestrial and marine, multi-taxa responses. Scientific Reports 8:1–9.

Ryo, M., C. A. Aguilar-Trigueros, L. Pinek, L. A. H. Muller, and M. C. Rillig. 2019. Basic Principles of Temporal Dynamics. Trends in Ecology and Evolution 34:723–733.

Sanford, E., J. L. Sones, M. García-Reyes, J. H. R. Goddard, and J. L. Largier. 2019. Widespread shifts in the coastal biota of northern California during the 2014–2016 marine heatwaves. Scientific Reports 9:1–14.

Selivanova, O. N. 2002. Marine Benthic Algae of the Russian Coasts of the Bering Sea (from Ozernoi Gulf to Dezhnev Bay , including Karaginskii Island). Constancea 83.

Smale, D. A., and T. Wernberg. 2013. Extreme climatic event drives range contraction of a habitat-forming species. Proceedings of the Royal Society B: Biological Sciences 280: 20122829.

Smale, D. A., T. Wernberg, E. C. J. Oliver, M. Thomsen, B. P. Harvey, S. C. Straub, M. T. Burrows, L. V. Alexander, J. A. Benthuysen, M. G. Donat, M. Feng, A. J. Hobday, N. J. Holbrook, S. E. Perkins-Kirkpatrick, H. A. Scannell, A. Sen Gupta, B. L. Payne, and P. J. Moore. 2019. Marine heatwaves threaten global biodiversity and the provision of ecosystem services. Nature Climate Change 9:306–312.

Smale, D. A., T. Wernberg, and M. A. Vanderklift. 2017. Regional-scale variability in the response of benthic macroinvertebrate assemblages to a marine heatwave. Marine Ecology Progress Series 568:17–30.

Spalding, M. D., H. E. Fox, G. R. Allen, N. Davidson, Z. A. Ferdaña, M. Finlayson, B. S. Halpern, M. A. Jorge, A. Lombana, S. A. Lourie, K. D. Martin, E. McManus, J. Molnar, C. A. Recchia, and J. Robertson. 2007. Marine ecoregions of the world: A bioregionalization of coastal and shelf areas. BioScience 57:573–583.

Spiecker, B. J., and B. A. Menge. 2022. El Niño and marine heatwaves: Ecological impacts on Oregon rocky intertidal kelp communities at local to regional scales. Ecological Monographs 92:1–26.

Suryan, R. M., M. L. Arimitsu, H. A. Coletti, R. R. Hopcroft, M. R. Lindeberg, S. J. Barbeaux, S. D. Batten, W. J. Burt, M. A. Bishop, J. L. Bodkin, R. Brenner, R. W. Campbell, D. A. Cushing, S. L. Danielson, M. W. Dorn, B. Drummond, D. Esler, T. Gelatt, D. H. Hanselman, S. A. Hatch, S. Haught, K. Holderied, K. Iken, D. B. Irons, A. B. Kettle, D. G. Kimmel, B. Konar, K. J. Kuletz, B. J. Laurel, J. M. Maniscalco, C. Matkin, C. A. E. McKinstry, D. H. Monson, J. R. Moran, D. Olsen, W. A. Palsson, W. S. Pegau, J. F. Piatt, L. A. Rogers, N. A. Rojek, A. Schaefer, I. B. Spies, J. M. Straley, S. L. Strom, K. L. Sweeney, M. Szymkowiak, B. P. Weitzman, E. M. Yasumiishi, and S. G. Zador. 2021. Ecosystem response persists after a prolonged marine heatwave. Scientific Reports 11:1–17.

Thomsen, M. S., L. Mondardini, T. Alestra, S. Gerrity, L. Tait, P. M. South, S. A. Lilley, and D. R. Schiel. 2019. Local Extinction of bull kelp (Durvillaea spp.) due to a marine heatwave. Frontiers in Marine Science 6:1–10.

Toyokokujigyo Corporation.1980. Second Basic Survey for Conservation of the Natural Environment Marine Area Survey Report of Marine Biological Survey (All parts of Japan Version). (in Japanese).

Watt, C. A., and R. A. Scrosati. 2013. Bioengineer effects on understory species richness, diversity, and composition change along an environmental stress gradient: Experimental and mensurative evidence. Estuarine, Coastal and Shelf Science 123:10–18.

Weitzman, B., B. Konar, K. Iken, H. Coletti, D. Monson, R. Suryan, T. Dean, D. Hondolero, and M. Lindeberg. 2021. Changes in Rocky Intertidal Community Structure During a Marine Heatwave in the Northern Gulf of Alaska. Frontiers in

Marine Science 8: 556820.

Wernberg, T., D. A. Smale, F. Tuya, M. S. Thomsen, T. J. Langlois, T. De Bettignies, S. Bennett, and C. S. Rousseaux. 2013. An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. Nature Climate Change 3:78–82.

Yamazaki, T. 2011. Molluscan Fauna of Akkeshi Marine Station: Part 1. Intertidal areas. Hokkaido University. (in Japanese).

Yoshida, T. 1998. Marine algae of Japan. Uchida Rokakuho Publishing, Tokyo. (in Japanese).

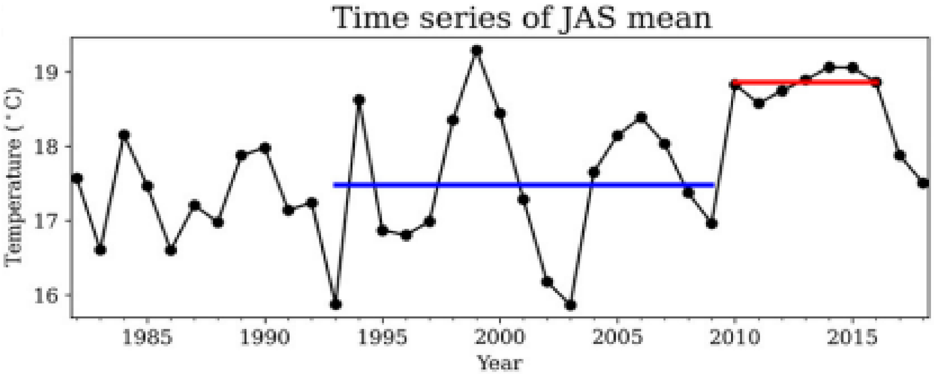


Fig. 3-1. Time series of the July–September mean sea surface temperature (°C) from 1982 to 2018 southeast of Hokkaido, Japan (143–147°E, 40–43°N). The blue line shows the 1993–2009 mean; the red line shows the 2010–2016 mean. (From Miyama et al. 2021a).

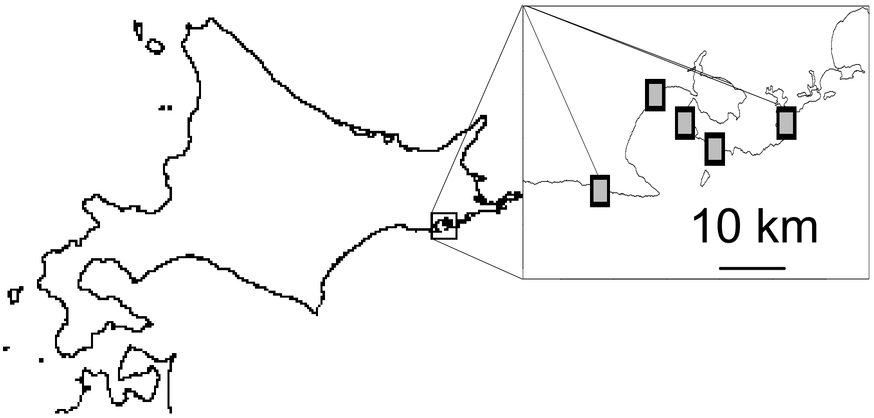


Fig. 3-2. Location of five rocky shores chosen for a census of intertidal organisms along the coast in southeast Hokkaido, Japan, along the Northwest Pacific Ocean.

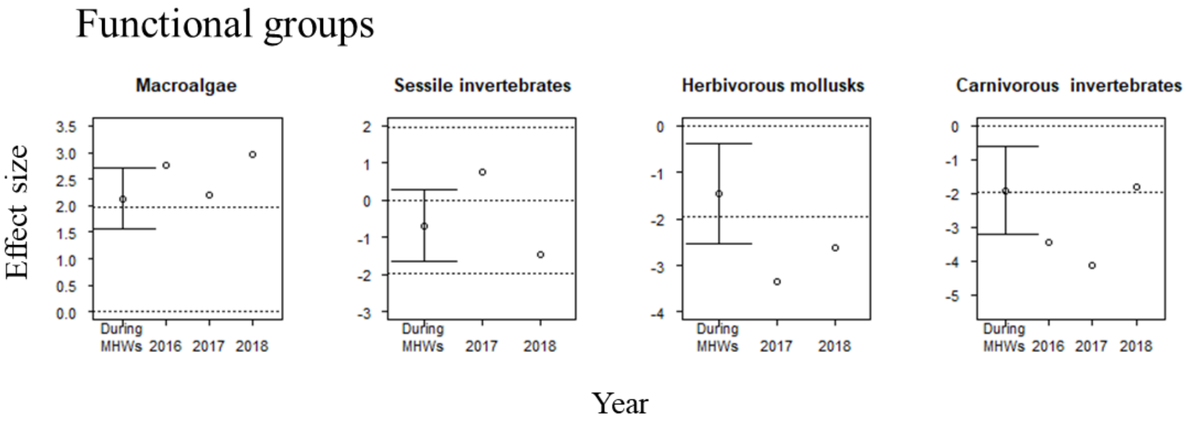


Fig. 3-3. Effect sizes of MHWs on the community abundance of four functional groups during the MHWs (2010–2016), in the last year of the MHWs (2016; shown only for functional groups where accumulative carryover effects were detected), and in the first (2017) and second (2018) years after the MHWs. The mean (±95% CI) is only presented for effect sizes during the MHWs. An abundance is significantly different from that before the MHWs if the 95% confidence interval does not cross the zero line or if the absolute value of the effect size exceeds 1.96 (where there is no confidence interval for the estimated effect size).

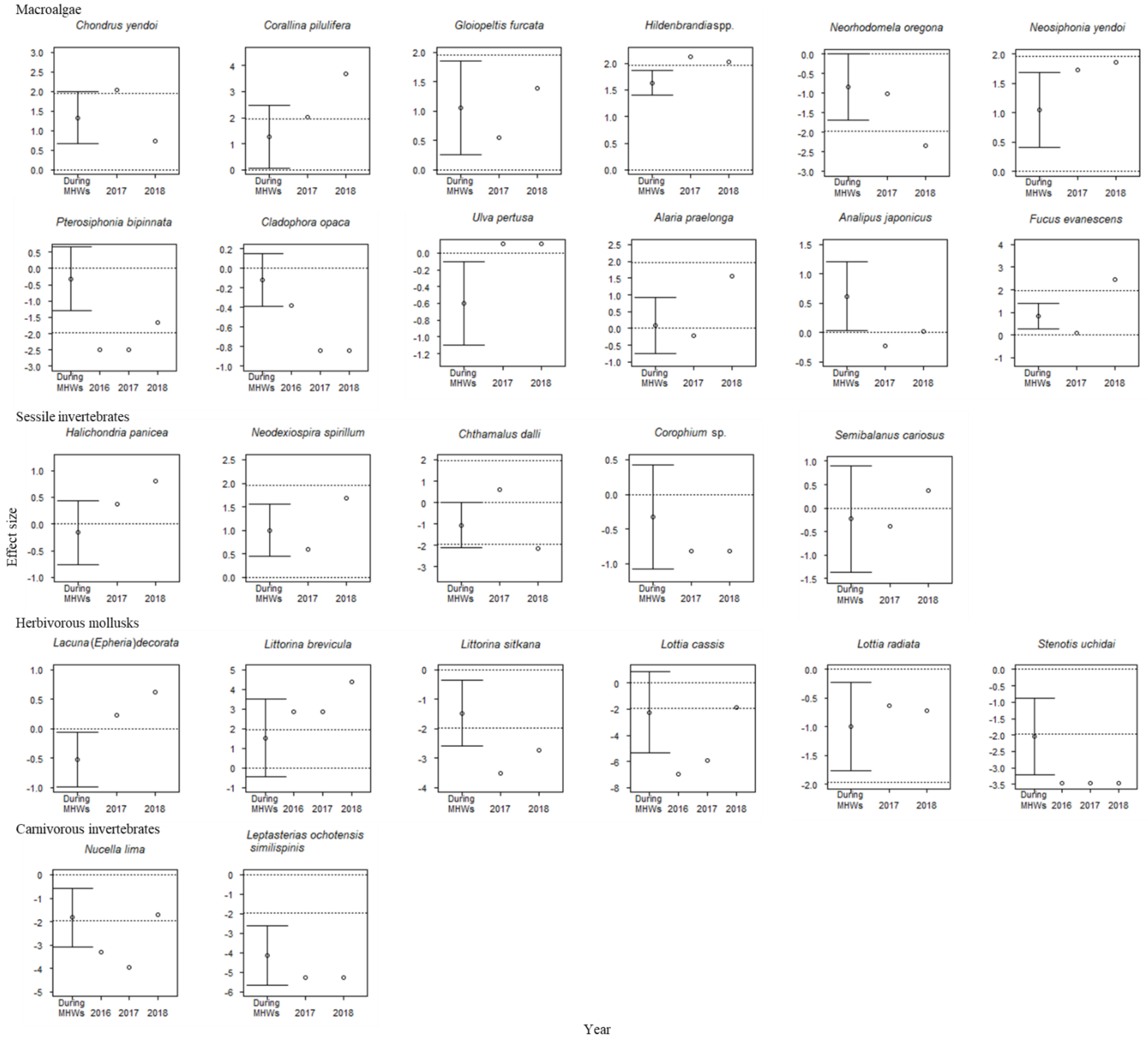


Fig. 3-4. Effect sizes of MHWs on the abundances of individual species during the MHWs (2010–2016), in the last year of the MHWs (2016; shown only for species where accumulative carryover effects were detected), and in the first (2017) and second (2018) years after the MHWs. The mean (±95% CI) is only presented for effect sizes during the MHWs. An abundance is significantly different from that before the MHWs if the 95% confidence interval does not cross the zero line or if the absolute value of the effect size exceeds 1.96 (where there is no confidence interval for the estimated effect size).

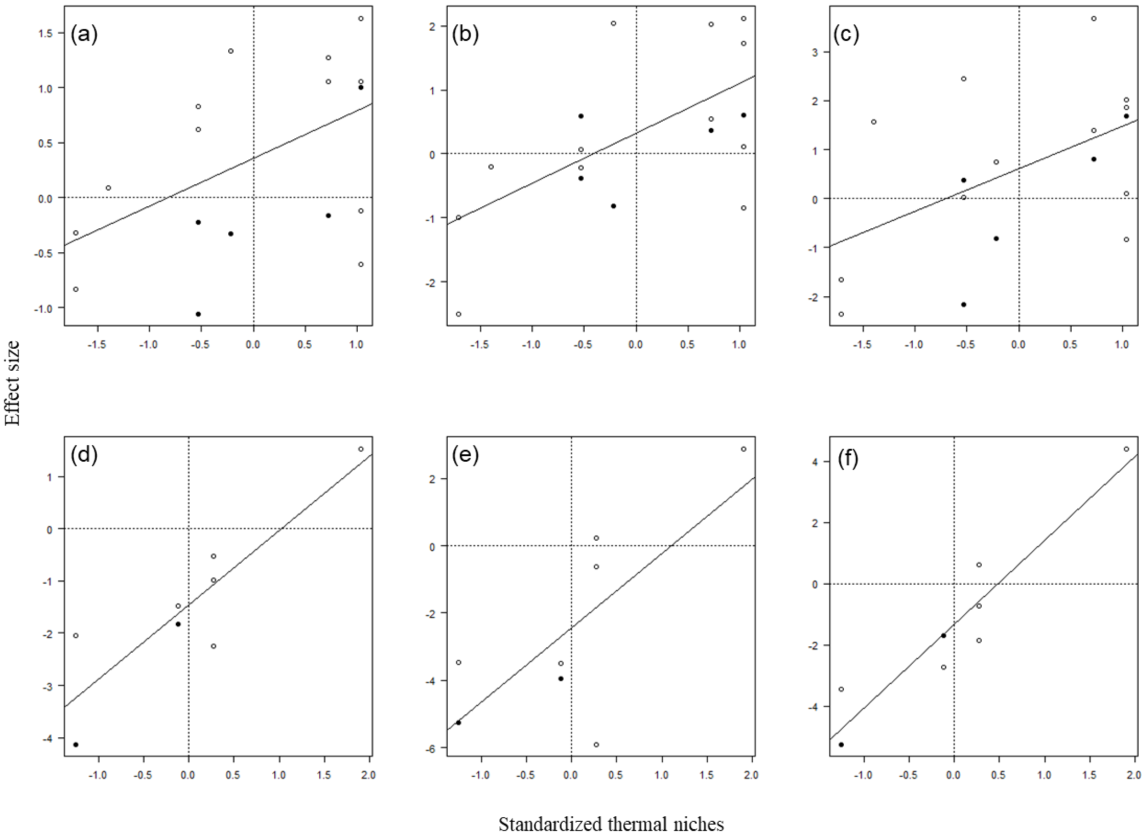


Fig. 3-5. Relationship between the effect size of MHWs on species abundances of sessile and mobile organisms during the MHWs, and in the first two years after the MHWs, and standardized thermal niches. Each plot includes the regression line for each model. (a) Sessile organisms during the MHWs, (b) sessile organisms in 2017, (c) sessile organisms in 2018, (d) mobile organisms during the MHWs, (e) mobile organisms in 2017, and (f) mobile organisms in 2018. The open circles in (a–c) indicate macroalgae and the filled circles indicate sessile invertebrates. The open circles in (d–f) indicate herbivorous mollusks, and the filled circles indicate carnivorous invertebrates.

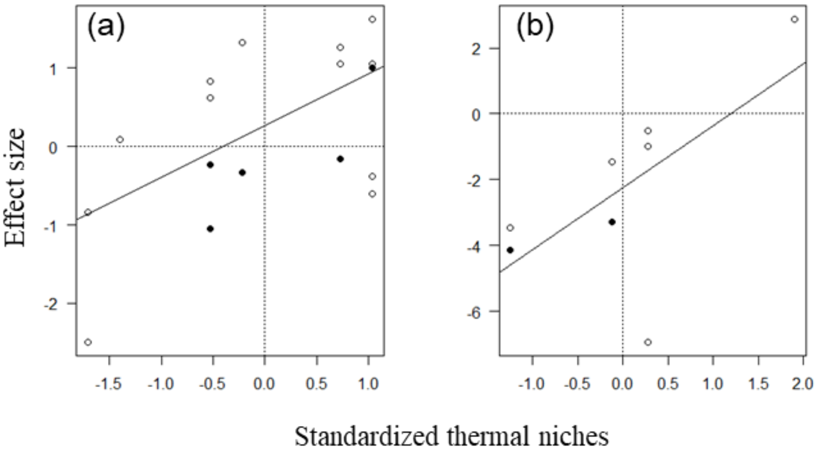


Fig. 3-6. Relationship between the effect size of MHWs on species abundances of sessile and mobile organisms in 2016 (i.e., considering accumulative carryover effects) and standardized thermal niches. Each plot includes the regression line for each model. (a) Sessile organisms and (b) mobile organisms. The open circles in (a) indicate macroalgae and the filled circles indicate sessile invertebrates. The open circles in (b) indicate herbivorous mollusks and the filled circles indicate carnivorous invertebrates.

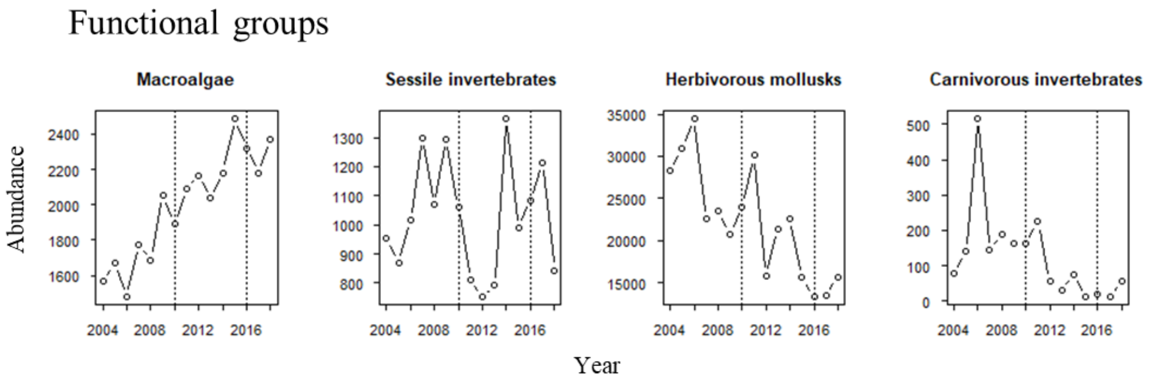


Fig. S3-1. The community abundance of each functional group of rocky intertidal organisms in southeast Hokkaido, Japan, from 2004 to 2018. The dashed vertical lines indicate the period of marine heatwaves (MHWs) from 2010 to 2016. Community abundance is the sum of the abundances of all species within a functional group at all survey sites for each year.

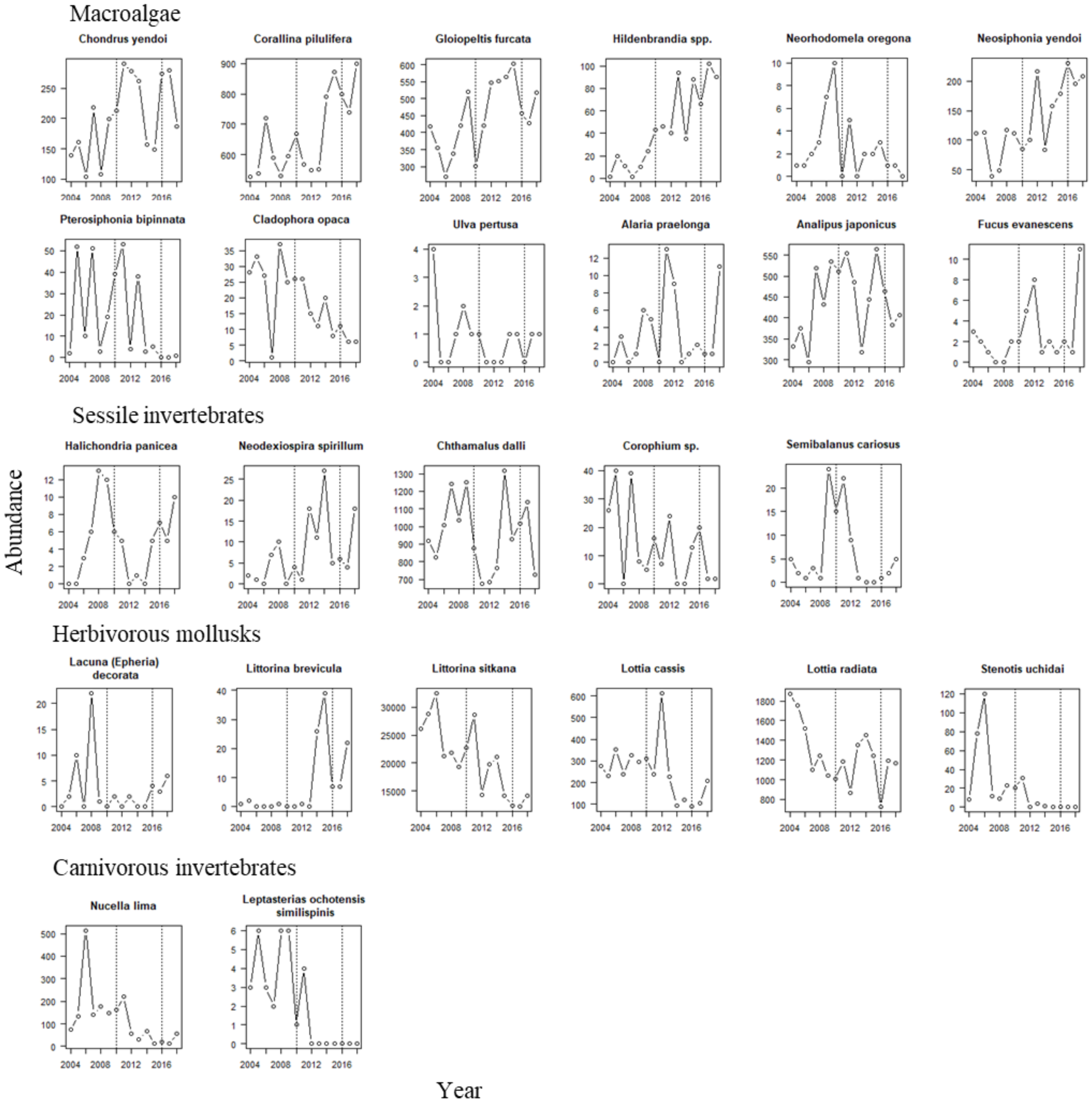


Fig. S3-2. The abundance of species in each of four functional groups of rocky intertidal organisms in southeast Hokkaido, Japan, from 2004 to 2018. The dashed vertical lines indicate the period of marine heatwaves (MHWs) from 2010 to 2016. Abundances were calculated by summing the abundance of each species at each census location for each year.

Table 3-1. Accumulative carryover effects of MHWs on the abundances of 25 species. Linear regression analysis treated the effect size of species abundance a response variable and the number of years (1–7) since the onset of MHWs as the explanatory variable. Shown are estimated coefficients for the intercept and slope (Estimate), standard errors (Std. error), and *p*-values (*P*). An accumulative carryover effect was considered present if the slope was significant and the intercept was not.

Functional group	Phylum	Taxon	Intercept			Slope		
			Estimate	Std. error	*P*	Estimate	Std. error	*P*
Macroalgae								
	Rhodophyta	*Chondrus yendoi*	1.86	0.79	0.07	-0.13	0.18	0.49
		Corallina pilulifera	-0.83	1.10	0.49	0.52	0.25	0.09
		Gloiopeltis furcata	-0.21	0.76	0.79	0.32	0.17	0.12
		Hildenbrandia spp.	1.35	0.25	< 0.001	0.07	0.06	0.28
		Neorhodomela oregona	-1.53	1.00	0.19	0.18	0.22	0.47
		Neosiphonia yendoi	-0.03	0.59	0.96	0.27	0.13	0.10
		Pterosiphonia bipinnata	1.65	0.71	0.07	-0.49	0.16	0.03
	Chlorophyta	*Cladophora opaca*	0.40	0.21	0.11	-0.13	0.05	0.04
		Ulva pertusa	-0.61	0.62	0.38	0.00	0.14	1.00
	Ochrophyta	*Alaria praelonga*	0.33	1.04	0.77	-0.06	0.23	0.81
		Analipus japonicus	0.83	0.73	0.31	-0.05	0.16	0.77
		Fucus evanescens	1.47	0.62	0.07	-0.16	0.14	0.30
Sessile invertebrates								
	Porifera	*Halichondria panicea*	-0.20	0.74	0.80	0.01	0.17	0.95
	Annelida	*Neodexiospira spirillum*	0.55	0.65	0.44	0.11	0.15	0.48
	Arthropoda	*Chthamalus dalli*	-2.57	1.11	0.07	0.38	0.25	0.19
		Corophium sp.	-0.15	0.94	0.88	-0.04	0.21	0.84
		Semibalanus cariosus	2.16	0.76	0.04	-0.60	0.17	0.02
Herbivorous mollusks								
	Mollusca	*Lacuna* (*Epheria*) *decorata*	-0.83	0.56	0.20	0.08	0.13	0.57
		Littorina brevicula	-2.39	1.52	0.18	0.98	0.34	0.03
		Littorina sitkana	0.55	0.96	0.59	-0.51	0.22	0.07
		Lottia cassis	3.73	2.48	0.19	-1.49	0.55	0.04
		Lottia radiata	-0.77	0.96	0.46	-0.06	0.21	0.81
		Stenotis uchidai	0.28	0.90	0.77	-0.58	0.20	0.03
Carnivorous invertebrates								
		Nucella lima	0.86	0.80	0.33	-0.67	0.18	0.01
	Echinodermata							
		Leptasterias ochotensis similispinis	-1.50	1.39	0.33	-0.66	0.31	0.09

Table 3-2. Accumulative carryover effects on community abundances of four functional groups of rocky intertidal organisms in southeast Hokkaido, Japan. For linear regression analysis, the effect size of community abundance was treated as the response variable and the number of years (1–7) since the onset of MHWs was the explanatory variable. Shown are estimated coefficients for the intercept and slope (Estimate), standard errors (Std. error), and *p*-values (*P*). An accumulative carryover effect was considered present if the slope was significant and the intercept was not.

Functional group	Intercept			Slope		
	Estimate	Std. error	*P*	Estimate	Std. error	*P*
Macroalgae	0.92	0.39	0.07	0.30	0.09	0.02
Sessile invertebrates	-1.60	1.13	0.21	0.23	0.25	0.40
Herbivorous mollusks	0.51	0.92	0.60	-0.49	0.21	0.06
Carnivorous invertebrates	0.85	0.87	0.38	-0.69	0.20	0.02

Table 3-3. Results of multiple regression analysis testing how the effects of MHWs on the abundance of each sessile species of rocky intertidal organism (macroalgae and sessile invertebrates) for each period differ depending on thermal and vertical niches. The response variables are the mean effect size during the MHWs (2010–2016), and the effect sizes in the first (2017) and second (2018) years after the MHWs. Explanatory variables include the estimated coefficients, standard errors, t-values, and *P*-values.

Response variable	Explanatory variable	Estimate	Std. error	t-value	*P*
Effect size of the abundance of sessile species during MHWs	Intercept	0.356	0.192	1.852	0.087
	Thermal niche	0.432	0.198	2.179	0.048
	Vertical niche	0.057	0.203	0.280	0.784
	Thermal niche × Vertical niche	0.262	0.223	1.175	0.261
Effect size of the abundance of sessile species in 2017	Intercept	0.322	0.256	1.259	0.230
	Thermal niche	0.784	0.264	2.974	0.011
	Vertical niche	-0.097	0.270	-0.358	0.726
	Thermal niche × Vertical niche	0.403	0.297	1.358	0.198
Effect size of the abundance of sessile species in 2018	Intercept	0.607	0.382	1.588	0.136
	Thermal niche	0.867	0.395	2.198	0.047
	Vertical niche	-0.242	0.404	-0.598	0.560
	Thermal niche × Vertical niche	0.469	0.444	1.057	0.310

Table 3-4. Results of linear regression analysis testing how the effects of MHWs on the abundance of each mobile species of rocky intertidal organism (herbivorous mollusks and carnivorous invertebrates) for each period differ depending on thermal niche. The response variables are the mean effect size during the MHWs (2010–2016), and the effect sizes in the first (2017) and second (2018) years after the MHWs. Explanatory variables include estimated coefficients, standard errors, t-values and *P*-values.

Response variable	Explanatory variable	Estimate	Std. error	t-value	*P*
Effect size of the abundance of mobile species during MHWs	Intercept	-1.463	0.291	-5.029	0.002
	Thermal niche	1.424	0.311	4.578	0.004
Effect size of the abundance of mobile species in 2017	Intercept	-2.448	0.773	-3.168	0.019
	Thermal niche	2.215	0.826	2.682	0.036
Effect size of the abundance of mobile species in 2018	Intercept	-1.338	0.366	-3.651	0.011
	Thermal niche	2.750	0.392	7.022	< 0.001

Table 3-5. Results of multiple regression analysis testing how the effects of MHWs on the abundance of each sessile species of rocky intertidal organism (macroalgae and sessile invertebrates) in 2016 (i.e., considering the accumulative carryover effect) differ depending on thermal and vertical niches. The response variable is the effect size obtained by considering accumulative carryover effects. Explanatory variables include estimated coefficients, standard errors, t-values, and *P*-values.

Response variable	Explanatory variable	Estimate	Std. error	t-value	*P*
Effect size of the abundance of sessile species	Intercept	0.266	0.207	1.288	0.220
	Thermal niche	0.661	0.213	3.101	0.008
	Vertical niche	-0.083	0.218	-0.381	0.709
	Thermal niche × Vertical niche	0.561	0.240	2.340	0.036

Table 3-6. Results of linear regression analysis testing how the effects of MHWs on the abundance of each mobile species (herbivorous mollusks and carnivorous invertebrates) in 2016 (i.e., considering the accumulative carryover effect) differ depending on thermal niche. The response variable is the effect size obtained by considering accumulative carryover effects. Explanatory variables include estimated coefficients, standard errors, t-values, and *P*-values.

Response variable	Explanatory variable	Estimate	Std. error	t-value	*P*
Effect size of the abundance of mobile species	Intercept	-2.240	0.852	-2.630	0.039
	Thermal niche	1.882	0.911	2.066	0.084

Table 3-7. Species niche traits of 25 species. Columns show species' thermal and vertical niches. Values of thermal and vertical niches are larger in species that inhabit warmer regions and higher elevations, respectively.

Functional group	Phylum	Taxon	Species niche traits	
			Thermal niche	Vertical niche
Macroalgae				
	Rhodophyta	*Chondrus yendoi*	9.6	5.3
		Corallina pilulifera	12.7	5.5
		Gloiopeltis furcata	12.7	11.9
		Hildenbrandia spp.	13.7	5.3
		Neorhodomela oregona	4.8	4.6
		Neosiphonia yendoi	13.7	10.9
		Pterosiphonia bipinnata	4.8	9.7
	Chlorophyta	*Cladophora opaca*	13.7	6.1
		Ulva pertusa	13.7	2.5
	Ochrophyta	*Alaria praelonga*	5.8	5.5
		Analipus japonicus	8.6	10.9
		Fucus evanescens	8.6	6.5
Sessile invertebrates				
	Porifera	*Halichondria panicea*	12.7	2.3
	Annelida	*Neodexiospira spirillum*	13.7	5.3
	Arthropoda	*Chthamalus dalli*	8.6	11.2
		Corophium sp.	9.6	7.6
		Semibalanus cariosus	8.6	9.0
Herbivorous mollusks				
	Mollusca	*Lacuna* (*Epheria*) *decorata*	9.6	-
		Littorina brevicula	13.7	-
		Littorina sitkana	8.6	-
		Lottia cassis	9.6	-
		Lottia radiata	9.6	-
		Stenotis uchidai	5.8	-
Carnivorous invertebrates				
		Nucella lima	8.6	-
	Echinodermata			
		Leptasterias ochotensis similispinis	5.8	-

Table S3-1. Linear trend of community abundances of four functional groups of rocky intertidal organisms in southeast Hokkaido, Japan. For linear regression analysis, the community abundance was treated as the response variable and the number of years (1–6) before the onset of MHWs was the explanatory variable. Shown are estimated coefficients for the intercept and slope (Estimate), standard errors (Std. error), and *p*-values (*P*).

Functional group	Intercept			Slope		
	Estimate	Std. error	*P*	Estimate	Std. error	*P*
Macroalgae	1427.47	138.17	< 0.001	79.49	35.48	0.09
Sessile invertebrates	824.20	115.82	0.002	74.09	29.74	0.07
Herbivorous mollusks	33893.00	3908.00	< 0.001	-2050.00	1004.00	0.11
Carnivorous invertebrates	185.40	162.96	0.32	5.46	41.85	0.90

Table S3-2. Abundances of four functional groups and 25 species of rocky intertidal organisms in southeast Hokkaido, Japan. Columns show the mean community abundance and that of 25 species for four functional groups before the marine heat waves (MHWs; 2004-2009), during the MHWs (2010-2016), and in 2016, 2017 and 2018.

Functional group	Phylum	Taxon	Abundance				
			Before	During		After	
			(mean)	(mean)	2016	2017	2018
Macroalgae			1705.7	2167.9	2320.0	2179.0	2370.0
	Rhodophyta	*Chondrus yendoi*	154.5	232.0	274.0	280.0	187.0
		Corallina pilulifera	583.3	686.0	800.0	739.0	900.0
		Gloiopeltis furcata	386.7	492.0	458.0	428.0	519.0
		Hildenbrandia spp.	11.2	58.9	66.0	102.0	90.0
		Neorhodomela oregona	4.0	1.9	1.0	1.0	0.0
		Neosiphonia yendoi	90.3	150.3	230.0	195.0	208.0
		Pterosiphonia bipinnata	22.8	20.3	0.0	0.0	1.0
	Chlorophyta	*Cladophora opaca*	25.2	16.7	11.0	6.0	6.0
		Ulva pertusa	1.3	0.4	0.0	1.0	1.0
	Ochrophyta	*Alaria praelonga*	2.5	3.7	1.0	1.0	11.0
		Analipus japonicus	414.8	477.4	463.0	384.0	407.0
		Fucus evanescens	1.3	3.0	2.0	1.0	11.0
Sessile invertebrates			1083.5	979.1	1085.0	1214.0	844.0
	Porifera	*Halichondria panicea*	5.7	3.4	7.0	5.0	10.0
	Annelida	*Neodexiospira spirillum*	3.3	10.3	6.0	4.0	18.0
	Arthropoda	*Chthamalus dalli*	1047.3	893.1	1016.0	1140.0	725.0
		Corophium sp.	19.7	11.4	20.0	2.0	2.0
		Semibalanus cariosus	6.0	6.9	1.0	2.0	5.0
Herbivorous mollusks			26719.3	20393.9	13247.0	13490.0	15611.0
	Mollusca	*Lacuna* (*Epheria*) *decorata*	5.8	1.1	4.0	3.0	6.0
		Littorina brevicula	0.7	11.0	7.0	7.0	22.0
		Littorina sitkana	24959.8	19012.7	12427.0	12183.0	14210.0
		Lottia cassis	286.3	241.6	88.0	105.0	207.0
		Lottia radiata	1422.7	1118.1	720.0	1189.0	1165.0
		Stenotis uchidai	41.7	8.0	0.0	0.0	0.0
Carnivorous invertebrates			204.5	82.7	20.0	13.0	55.0
		Nucella lima	197.8	80.6	20.0	13.0	55.0
	Echinodermata						
		Leptasterias ochotensis similispinis	4.3	0.7	0.0	0.0	0.0

Table S3-3. The effect sizes of marine heatwaves (MHWs) on abundances of four functional groups and 25 species of rocky intertidal organisms in southeast Hokkaido, Japan. Columns show mean and 95% confidence intervals of the effect size of MHWs on the community abundance and that of 25 species for four functional groups during the MHWs (2010-2016), and in 2016, 2017 and 2018.

Functional group	Phylum	Taxon	Effect size				
			During MHWs			After MHWs	
			Mean	95% CIs	2016	2017	2018
Macroalgae			2.14	0.58	2.76	2.21	2.95
	Rhodophyta	*Chondrus yendoi*	1.33	0.67	1.97	2.04	0.74
		Corallina pilulifera	1.27	1.22	2.70	2.03	3.68
		Gloiopeltis furcata	1.06	0.79	0.84	0.54	1.40
		Hildenbrandia spp.	1.63	0.23	1.77	2.12	2.02
		Neorhodomela oregona	-0.83	0.85	-1.00	-1.00	-2.35
		Neosiphonia yendoi	1.05	0.64	2.06	1.73	1.86
		Pterosiphonia bipinnata	-0.32	0.97	-2.50	-2.50	-1.66
	Chlorophyta	*Cladophora opaca*	-0.12	0.27	-0.38	-0.84	-0.84
		Ulva pertusa	-0.61	0.50	-1.14	0.11	0.11
	Ochrophyta	*Alaria praelonga*	0.09	0.83	-0.20	-0.20	1.56
		Analipus japonicus	0.62	0.59	0.56	-0.22	0.02
		Fucus evanescens	0.83	0.56	0.66	0.06	2.45
Sessile invertebrates			-0.68	0.97	0.08	0.77	-1.47
	Porifera	*Halichondria panicea*	-0.16	0.60	0.58	0.37	0.80
	Annelida	*Neodexiospira spirillum*	1.00	0.55	0.89	0.60	1.69
	Arthropoda	*Chthamalus dalli*	-1.05	1.08	-0.12	0.58	-2.17
		Corophium sp.	-0.33	0.75	0.43	-0.82	-0.82
		Semibalanus cariosus	-0.23	1.13	-0.86	-0.38	0.37
Herbivorous mollusks			-1.45	1.08	-3.44	-3.35	-2.62
	Mollusca	*Lacuna* (*Epheria*) *decorata*	-0.52	0.46	0.38	0.22	0.62
		Littorina brevicula	1.53	1.99	2.88	2.88	4.41
		Littorina sitkana	-1.47	1.12	-3.41	-3.51	-2.74
		Lottia cassis	-2.25	3.11	-6.95	-5.90	-1.86
		Lottia radiata	-0.99	0.77	-2.68	-0.63	-0.71
		Stenotis uchidai	-2.04	1.18	-3.45	-3.45	-3.45
Carnivorous invertebrates			-1.91	1.31	-3.44	-4.14	-1.82
		Nucella lima	-1.83	1.25	-3.29	-3.95	-1.71
	Echinodermata						
		Leptasterias ochotensis similispinis	-4.13	1.53	-5.25	-5.25	-5.25

Chapter 4

General Discussion

In this chapter, I first summarize the findings from Chapters 1, 2 and 3, then, discuss the influence of ocean current fluctuation on the marine community dynamics.

4.1. Summary of Chapters 1, 2 and 3

In Chapter 1, I reviewed previous studies that examined community dynamics. First, I reviewed studies of community dynamics in general. The result showed that the quantification of community dynamics has been conducted using a variety of aggregate properties (community abundance, and diversity), univariate non-aggregate properties (individual species abundances), and multivariate non-aggregate properties (community composition), and the objectives of community dynamics research have been (1) to deepen our understanding of the variability of ecosystem, community, and population dynamics and its driving mechanisms, and (2) to deepen our understanding of many key ecological phenomena such as stability, succession, community assembly and synchrony, and (3) to elucidate the driving mechanisms of community dynamics. Next, I reviewed the studies on marine community dynamics. The results indicated that most studies of community dynamics in marine communities have evaluated the effects of anthropogenic disturbance based on experiments, and few studies have evaluated the effects of natural disturbance. Future work should use long-term continuous community data, including periods before and after natural disturbances, to determine the effects of natural disturbances on community dynamics. In particular, the focus on natural disturbances such as ocean current fluctuations, eruption, marine heatwave, ice scour, and freshwater flooding, which have rarely evaluated as drivers of community dynamics, may provide previously unexplored insights into the factors that influence community dynamics. Among these disturbances, ocean current fluctuations occur over a wide area and have a large spatial range of influence. In addition, ocean current fluctuations are also associated with the occurrence of marine heatwaves (e.g., Miyama et al. 2021). The effects of ocean current fluctuations on marine community dynamics are therefore of particular importance for future research. Finally, the target system was examined to determine the effect of the ocean current on community dynamics, and it was shown that the rocky intertidal community is one of the ideal model systems.

In Chapter 2, I investigated spatial variation in patterns of a long-term trajectory of natural communities and spatial variation in temporal variability of species richness, species composition, and community abundance, as well as their interdependence in the rocky intertidal sessile communities of the Pacific coast of Japan. I analyzed 16-year census data for intertidal communities from 30 rocky shores along Japan's Pacific coast to assign community change to four possible trajectories (stable, reversible, abrupt, or linear) representing different aspects of ecological resilience, and to estimate multiple metrics of temporal invariability (species richness, species composition, and community abundance). I examined (1) how the prevalence of the four trajectories differs among regions, (2) how the features (model coefficients) of each trajectory vary among regions, and (3) how the temporal variabilities differ among trajectories and regions. I found that the stable trajectory was the most common. Its features differed among regions, with a faster recovery to steady-state equilibrium in low-latitude regions). Furthermore, trajectories and temporal invariabilities both varied among regions, seemingly in association with the strength of ocean current fluctuations. In regions where fluctuations in the flow patterns of the ocean current are greater, temporal variability in species richness and species composition is greater, while temporal variability in community abundance is smaller. Temporal variability of species composition was greater near the Kuroshio Current than near the Oyashio, while temporal variability of community abundance was the opposite.

In Chapter 3, I evaluated the response of rocky intertidal communities to marine heat waves caused by ocean current fluctuations. I examined the impacts of MHWs that occurred in southeastern Hokkaido, northern Japan, in summer (July–September) from 2010 to 2016 on rocky intertidal communities by separating the effects of environmental stochasticity from that of MHW. (1) Did MHWs have accumulative carryover effects (i.e., continued increase or decrease in abundance with the number of years elapsed since the onset of the MHWs) on community abundance and abundance of each species of the four functional groups: macroalgae, sessile invertebrates, herbivorous invertebrates, and predatory invertebrates? (2) How did the effects of the MHWs on community abundance of the four functional groups (during the MHWs (2010-2016) and subsequent recovery (first year (2017) and two years after the MHWs (2018)) differ? (3) How does the susceptibility to MHWs differ depending on the species niche (thermal and vertical) traits? I found that the accumulative carryover effects of MHWs were detected both in the functional group abundance and in the abundance of each species. In some species, the effects of MHWs could be underestimated if accumulative carryover effects were not considered. While previous studies have reported that MHWs decline macroalgae and increase sessile invertebrates in the rocky intertidal habitats, the results of present study show that macroalgae increased during and after MHWs, while sessile invertebrates did not respond during and after MHWs. Herbivorous mollusks decreased during and after MHWs. Carnivorous invertebrates declined during MHWs and in the first year after MHWs. During and after MHWs, abundances of species with low thermal niches decreased and those with high thermal niches increased. The increase in abundance in warmer-water species due to MHWs is more pronounced for species with higher vertical niches, only when accumulative carryover effects were considered. These results emphasize that it is essential to consider accumulative carryover effects when assessing the response of marine organisms to MHWs and that more reports on the response of marine organisms to MHWs are needed for various systems, regions and organisms to predict the response of marine organisms.

4.2. Effects of ocean current fluctuations on community dynamics of marine organisms

My study revealed that ocean current fluctuations drive both spatial (Chapter 2) and temporal (Chapter 3) variation in the dynamics of rocky intertidal communities. This important role of ocean current fluctuations as a driver of marine community dynamics may be universal in marine ecosystems. This is because spatiotemporal variations in ocean currents have been shown to cause fluctuations in the abundance of various marine organisms living in both the pelagic and benthic habitats, such as macro algae (Taniguchi et al. 1986; Johnson et al. 2011; Liu et al. 2013; Liu et al. 2015; Li et al. 2017), zooplankton (Johnson et al. 2011), hydrozoa (Lo et al. 2014), corals (Nomura and Hirabayashi. 2018; Keshavmurthy et al. 2019), mollusk (Kawajiri et al. 1981; Kurihara. 2007; Takami et al. 2008; Johnson et al. 2011; Liu et al. 2015), starfishes (Yamaguchi. 1986), sea urchins (Nomura and Hirabayashi. 2018; Ohgaki et al. 2019), lobsters (Johnson et al. 2011) and fishes (Murase. 2013; Monaco et al. 2021). However, since most of the evidence is obtained at the population level of single species or few species (Kawajiri et al. 1981; Yamaguchi. 1986; Taniguchi et al. 1986; Takami et al. 2008; Liu et al. 2013; Liu et al. 2015; Li et al. 2017; Ohgaki et al. 2019), an assessment of the importance of ocean current fluctuations as a driver of marine community dynamics will have to await future research.

My study shows that analysis using both aggregate properties, univariate and multivariate nonaggregate properties, provides a comprehensive understanding of the impact of ocean current fluctuations on the community dynamics of rocky intertidal organisms and a greater understanding of the processes and mechanisms behind that impact. In Chapter 2, the response of community dynamics to ocean current fluctuation was evaluated by stability quantified by aggregate properties (species richness and community abundance) and multivariate non-aggregate properties (species composition). The results revealed that the increase in ocean current fluctuation resulted in an increase in the species replacement rate, but did not result in an increase in the temporal variability of this community abundances. In Chapter 3, I examined the response of communities quantified by aggregate properties (community abundances of functional groups) and univariate non-aggregate properties (abundances of individual species) to marine heat waves caused by ocean current fluctuations. The results indicate that differences in community abundance responses to marine heat waves for each functional group can be explained by differences in the thermal niche of the species that compose each of them. Thus, when evaluating the effects of ocean current fluctuations on community dynamics, it is recommended to take an approach similar to that used in this study, where multiple properties are quantified at the same time.

My study demonstrates that long-term data over a period of 10 years is extremely useful in assessing the effects of ocean current fluctuations on community dynamics. First, long-term data will allow us to answer a greater number of scientific questions about the effects of ocean current fluctuations on community dynamics. In Chapter 2, I successfully clarified the effect of ocean current fluctuations on ecological resilience because sufficient time-series data were available for the analysis. While it was not applied in my study, Empirical dynamic modellings, which are the powerful tools to detect causal relationships, also require long time-series data (Ushio et al. 2018). Second, long-term data will allow us to accurately assess the effects of ocean current fluctuations on community dynamics. In Chapter 3, long-term data allowed us to evaluate the effects of marine heat waves caused by ocean current fluctuations on the community by separating the effects of environmental stochasticity from that of MHW. Using long-term data, I successfully detected an accumulative carryover effect in marine communities caused by marine heat waves that occurred for seven consecutive years. Thus, despite the outstanding efficacy of long-term data over 10 years to assess the effects of ocean current fluctuations on community dynamics, many previous studies have been conducted over relatively short time series of less than 10 years (Taniguchi et al. 1986; Kurihara. 2007; Takami et al. 2008; Murase. 2013; Lo et al. 2014; Nomura and Hirabayashi. 2018).

Currently, changes in the ocean environment are ongoing due to global warming, such as changes in the pattern of ocean current fluctuations and associated changes in the occurrence of heat waves. Therefore, it is important to understand the response of community dynamics to ocean current fluctuations. In elucidating the response of community dynamics to ocean current fluctuations, the knowledge lacking in previous studies, including this study (Chapters 2 and 3), is how species traits other than thermal niche are related to the susceptibility to ocean current. Ocean currents are characterized not only by temperature but also by environmental factors such as nutrient, salinity, and primary productivity (e.g., Qiu. 2001; Sakurai. 2007; Yatsu et al. 2013). In addition, ocean currents are passive transport systems for marine organisms (Yamaguchi. 1986; Johnson et al. 2011; Lo et al. 2014). Therefore, future studies are needed to evaluate and predict the effects of ocean current fluctuations on community dynamics, taking into account species traits such as temperature, nutrient, salinity, primary productivity, ease of transport of the organism of interest and susceptibility of effect by the transported organism.

References

Johnson, C. R., S. C. Banks, N. S. Barrett, F. Cazassus, P. K. Dunstan, G. J. Edgar, S. D. Frusher, C. Gardner, M. Haddon, F. Helidoniotis, K. L. Hill, N. J. Holbrook, G. W. Hosie, P. R. Last, S. D. Ling, J. Melbourne-Thomas, K. Miller, G. T. Pecl, A. J. Richardson, K. R. Ridgway, S. R. Rintoul, D. A. Ritz, D. J. Ross, J. C. Sanderson, S. A. Shepherd, A. Slotwinski, K. M. Swadling, and N. Taw. 2011. Climate change cascades: Shifts in oceanography, species' ranges and subtidal marine community dynamics in eastern Tasmania. Journal of Experimental Marine Biology and Ecology 400:17–32.

Kawajiri, M., T. Sasaki, and Y. Kageyama. 1981. Extensive deterioration of Ecklonia kelp stands and death of the plants, and fluctuations in abundance of the abalone off Toji, southern Izu peninsula. Bulletin of the Shizuoka Prefectural Fisheries Experiment Station 15: 19–30 (in Japanese).

Keshavmurthy, S., C. Y. Kuo, Y. Y. Huang, R. Carballo-Bolaños, P. J. Meng, J. T. Wang, and C. A. Chen. 2019. Coral reef resilience in Taiwan: Lessons from long-term ecological research on the coral reefs of Kenting National Park (Taiwan). Journal of Marine Science and Engineering 7: 388.

Kurihara, T. 2007. Spatiotemporal variations in rocky intertidal malacofauna throughout

Japan in the 1970s and 1980s. Marine Biology 153:61–70.

Li, J. J., Z. M. Hu, X. Gao, Z. M. Sun, H. G. Choi, D. L. Duan, and H. Endo. 2017. Oceanic currents drove population genetic connectivity of the brown alga Sargassum thunbergii in the north-west Pacific. Journal of Biogeography 44:230–242.

Liu , Y., S. I. Saitoh, N. Radiarta, T. Isada, T. Hirawake, H. Mizuta, and H. Yasui. 2013. Improvement of an aquaculture site-selection model for Japanese kelp (Saccharina japonica) in southern Hokkaido, Japan: an application for the impacts of climate events. ICES Journal of Marine Science 70:1460–1470.

Liu, Y., S. I. Saitoh, S. Nakada, X. Zhang, and T. Hirawake. 2015. Impact of oceanographic environmental shifts and atmospheric events on the sustainable development of coastal aquaculture: A case study of kelp and scallops in Southern Hokkaido, Japan. Sustainability 7:1263–1279.

Lo, W. T., S. F. Yu, and H. Y. Hsieh. 2014. Hydrographic processes driven by seasonal monsoon system affect siphonophore assemblages in tropical-subtropical waters (western North Pacific Ocean). PLoS ONE 9.

Miyama, T., S. Minobe, and H. Goto. 2021. Marine Heatwave of Sea Surface Temperature of the Oyashio Region in Summer in 2010–2016. Frontiers in Marine Science 7:1–13.

Monaco, C. J., D. J. Booth, W. F. Figueira, B. M. Gillanders, D. S. Schoeman, C. J. A. Bradshaw, and I. Nagelkerken. 2021. Natural and anthropogenic climate variability shape assemblages of range-extending coral-reef fishes. Journal of Biogeography 48:1063−1075.

Murase, A. 2013. Community structure and short temporal stability of a rockpool fish assemblage at Yaku-shima Island, southern Japan, northwestern Pacific. Ichthyological Research 60:312–326.

Nomura, K., and I. Hirabayashi. 2018. Mass mortality of coral communities caused by abnormality low water temperature observed at Kii peninsula west coast for winter season in 2018. Marine Pavilion Supplement 7: 1–14 (in Japanese).

Ohgaki, S. I., T. Kato, N. Kobayashi, H. Tanase, N. H. Kumagai, S. Ishida, T. Nakano, Y. Wada, and Y. Yusa. 2019. Effects of temperature and red tides on sea urchin abundance and species richness over 45 years in southern Japan. Ecological Indicators 96:684–693.

Qiu, B. 2001. Kuroshio and Oyashio currents. In Ocean Currents: A Derivative of the Encyclopedia of Ocean Sciences (eds Steele, J. H. et al.) 1413–1425 (Academic Press, 2001).

Sakurai, Y. 2007. An overview of the Oyashio ecosystem. Deep-Sea Research Part II: Topical Studies in Oceanography 54:2526–2542.

Takami, H., T. Saido, T. Endo, T. Noro, T. Musashi, and T. Kawamura. 2008. Overwinter mortality of young-of-the-year Ezo abalone in relation to seawater temperature on the north Pacific coast of Japan. Marine Ecology Progress Series 367:203–212.

Taniguchi, K., M. Sato, and K. Owada. 1986. On the characteristics of the structural variation in the Eisenia bicyclis population on Joban coast, Japan. Bulletin of Tohoku National Fisheries Researh Institute 48: 49–57 (in Japanese with English abstract).

Ushio, M., C. H., Hsieh, R., Masuda, E. R.,Deyle, H., Ye, C. W., Chang, G. Sugihara and M. Kondoh. 2018. Fluctuating interaction network and time-varying stability of a natural fish community. Nature, 554: 360–363.

Yamaguchi, M. 1986. Acanthaster planci infestations of reefs and coral assemblages in Japan: a retrospective analysis of control efforts. Coral Reefs 5:23–30.

Yatsu, A., S. Chiba, Y. Yamanaka, S. I. Ito, Y. Shimizu, M. Kaeriyama, and Y.

Watanabe. 2013. Climate forcing and the Kuroshio/Oyashio ecosystem. ICES Journal of Marine Science 70:922–933.