



## Original article

# Contribution of environmental and spatial processes to rocky intertidal metacommunity structure

Takehiro Okuda<sup>a,b,\*</sup>, Takashi Noda<sup>b</sup>, Tomoko Yamamoto<sup>c</sup>, Masakazu Hori<sup>d</sup>, Masahiro Nakaoka<sup>e</sup>

<sup>a</sup> Tohoku National Fisheries Research Institute, Fisheries Research Agency, Same-machi, Hachinohe, Aomori 031-0841, Japan

<sup>b</sup> Faculty of Environmental Earth Science, Hokkaido University, N10W5, Kita-ku, Sapporo, Hokkaido 060-0810, Japan

<sup>c</sup> Faculty of Fisheries Sciences, Kagoshima University, Arata 4-50-20, Simoarata, Kagoshima 890-0056, Japan

<sup>d</sup> National Research Institute of Fisheries and Environment of Inland Sea, Fisheries Research Agency, Maruishi 2-17-5, Hatsukaichi, Hiroshima 739-0452, Japan

<sup>e</sup> Akkeshi Marine Station, Field Science Center for Northern Biosphere, Hokkaido University, Aikappu, Akkeshi, Hokkaido 088-1113, Japan

## ARTICLE INFO

## Article history:

Received 9 November 2009

Accepted 16 April 2010

Published online 11 May 2010

## Keywords:

$\beta$ -Diversity

Ecological traits

Environmental heterogeneity

Macro ecology

Spatial structure

Variation partitioning

## ABSTRACT

It has been debated whether the community structure of an open system is more dependent on environmental processes associated with niche explanations, or on spatial processes related to dispersal. Their relative importance may differ among taxonomic groups with properties of the community such as ecological characteristics (e.g., dispersal ability and life history) and habitat type. We examined the relative importance of environmental and spatial processes on community structure for three taxonomic groups with different ecological characteristics (macroalgae, sessile invertebrates, and mobile molluscs) in rocky intertidal shores of Sanriku Coast, Japan. To evaluate the relative contribution of the two processes in determining community structure, we conducted variation partitioning to reveal the degree of variation of community structure (i.e.,  $\beta$ -diversity) explained by environmental heterogeneity and spatial arrangement of local communities. The results of our analyses indicated that  $\beta$ -diversity was significantly explained by both environmental factors (macroalgae, 29.3% of community variation: sessile animal, 40.7%; mobile molluscs, 16.7%) and spatial factors (macroalgae, 19.9%; sessile animal, 3.6%; mobile molluscs, 6.6%) in all taxonomic groups. These results imply that although some taxonomic groups live in the same ecosystem, share common resources, and interact with each other, the mechanisms determining their community structure change depending on ecological characteristics such as dispersal ability and life history.

© 2010 Elsevier Masson SAS. All rights reserved.

## 1. Introduction

In recent years, community ecology has moved toward a greater understanding of open systems such as metacommunities which are defined as sets of local communities linked by the dispersal of multiple potentially interacting species (e.g., [Leibold et al., 2004](#); [Wilson, 1992](#)). Previous studies focusing on open systems have debated the relative importance of environmental processes associated with niche explanations and spatial processes related to dispersal in determining community structure (e.g., [Cottenie, 2005](#); [Leibold et al., 2004](#)). Diverse analytical methods have been used to

investigate the relative contributions of environmental heterogeneity and spatial structure of local communities, which reflect the influence of environmental and spatial processes, respectively, in determining community structure in various taxa and habitats (e.g., [Borcard et al., 1992](#)).

Both environmental and spatial processes are closely related to the ecological characteristics of organisms. For example, four conceptual models describing metacommunity dynamics are distinguished not only by environmental heterogeneity and inter-patch movement, but also by similarity of species traits ([Table 1](#): see details in [Holyoak et al., 2005](#)). Therefore, to fully understand the determinants of community structure, we should explicitly consider the ecological characteristics of organisms ([Kearney, 2006](#); [McGill et al., 2006](#)). Comparing the relative contributions among taxonomic groups with different ecological characteristics could provide the first step revealing the generality and variability of mechanisms that determine community structure ([Beisner et al., 2006](#); [Cottenie, 2005](#)).

[Cottenie \(2005\)](#) conducted a meta-analysis by collecting 158 published datasets with information on community structure,

\* Corresponding author at: Tohoku National Fisheries Research Institute, Fisheries Research Agency, Same-machi, Hachinohe, Aomori 031-0841, Japan. Tel.: +81 178 33 1500; fax: +81 178 34 1357.

E-mail addresses: [okudy@affrc.go.jp](mailto:okudy@affrc.go.jp) (T. Okuda), [noda@ees.hokudai.ac.jp](mailto:noda@ees.hokudai.ac.jp) (T. Noda), [yamamoto@fish.kagoshima-u.ac.jp](mailto:yamamoto@fish.kagoshima-u.ac.jp) (T. Yamamoto), [mhori@fra.affrc.go.jp](mailto:mhori@fra.affrc.go.jp) (M. Hori), [nakaoka@fsc.hokudai.ac.jp](mailto:nakaoka@fsc.hokudai.ac.jp) (M. Nakaoka).

<sup>1</sup> Present address: National Research Institute of Far Seas Fisheries, Fisheries Research Agency, Fukuura 2-12-4, Kanazawa-ku, Yokohama, 236-8648, Japan. Tel.: +81 45 788 7502; fax: +81 45 788 5004.

**Table 1**

A brief comparison of four conceptual models of metacommunity. This table focuses on environmental condition of each local patch, inter-patch movement, and species traits: see details in Holyoak et al. (2005). Patch dynamics model extends meta-population model for patch dynamics to more than two species. Species sorting model emphasize that resource gradients or patch types cause sufficiently strong differences in the local demography and interaction of species. Mass effects model represents a multispecies version of source-sink dynamics and rescue effects. Neutral model assumes that all species are similar in their competitive ability, movement, and fitness. Inter-patch movement involves both connectivity among local patches and dispersal ability of organisms. In this table, species traits include all ecological characteristics of organisms; e.g., competition ability, environmental tolerance, life history, and dispersal ability.

Characteristic	Patch dynamics	Species sorting	Mass effects	Neutral model
Patch condition	Similar	Dissimilar	Dissimilar	Similar
Inter-patch movement	Low rate	Not specified	Higher	Localized
Species traits	Similar or dissimilar	Dissimilar	Dissimilar	Similar

environmental, and spatial variables to examine the relative role of environmental and spatial factors in determining community structure among different types of organisms. Cottenie (2005) found that environmental heterogeneity related to niche explanations tended to be more important to community structure than spatial arrangement associated with dispersal processes, but the relative importance of these two mechanisms varied depending on community characteristics such as ecological characteristics (e.g., dispersal ability) and habitat types. However, such a comparison using datasets collected from different systems cannot distinguish between the influence of ecological characteristics of communities and biotic and abiotic features of habitats on the relative role of environmental and spatial factors in determining community structure. Both the characteristics of organisms and the structure of landscapes may vary depending on each studied group (Beisner et al., 2006). Therefore, to control for differences in landscape structure and to separate the relative roles of environmental and spatial processes, we need to focus on taxonomic groups with different ecological characteristics within the same ecosystem (Beisner et al., 2006).

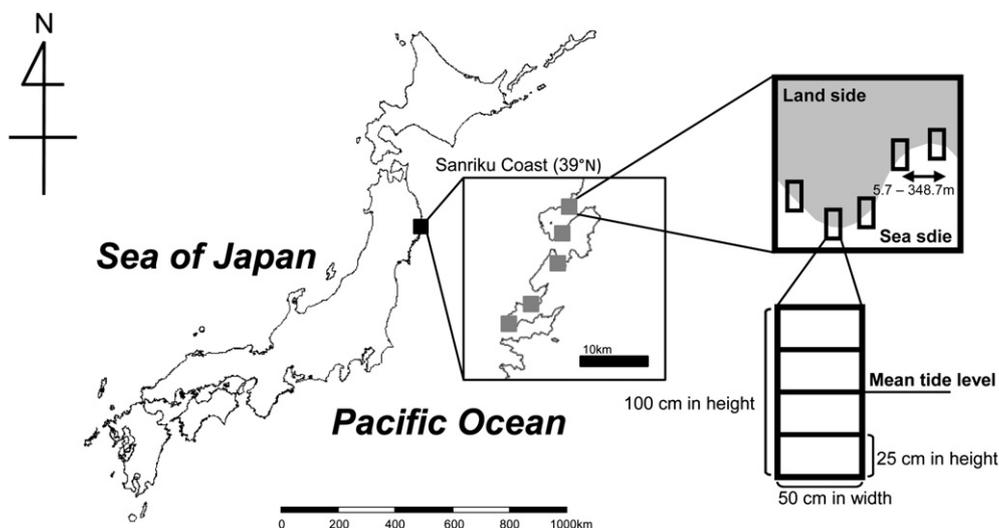
In this study, we examine the relative importance of environmental and spatial processes on community structure for three taxonomic groups with different ecological characteristics

(macroalgae, sessile animals, and mobile molluscs) on the rocky intertidal shore of Sanriku Coast, Japan. Rocky intertidal assemblages are one of the best systems with which to compare the relative contribution of environmental and spatial processes on determining community structure among taxonomic groups because of following reasons. Three taxonomic groups focused in this study (macroalgae, sessile animals, and mobile molluscs) have different ecological characteristics such as trophic level, life history, and dispersal ability. Furthermore, local community patterns and their causal processes can be closely studied (see Menge and Branch, 2001 for review). Lastly, the effects of both abiotic and biotic environmental factors on distribution and abundances of organisms are well investigated (e.g., Connell, 1961; Menge, 1995; Menge and Sutherland, 1987; Paine, 1966). Specifically, by focusing dispersal ability of taxonomic groups, we expect that community structure is under greater influence from spatial factors in taxonomic groups with lower dispersal ability (macroalgae) than groups with greater dispersal ability (sessile animals and mobile molluscs). Inter-patch movement related to dispersal ability is one of the key components in understanding of open systems such as metacommunities. In addition, we show the importance of each environmental (abiotic and biotic) factor and scale of geographic arrangement of local communities in determining community structure.

## 2. Materials and methods

### 2.1. Census design

Macroalgae, sessile animals, and mobile molluscs were surveyed along five shores of Sanriku Coast (39°N, 142°E), Japan (Fig. 1). Distance intervals between neighboring shores ranged from 4.1 to 25.7 km. Within each shore, five census plots were placed on rock walls at semi-exposed locations with intervals between neighboring plots ranging from 5.7 to 348.7 m (mean ± standard deviation [SD]: 87.3 ± 85.5 m). Each plot was 50 cm wide by 100 cm high; the middle of the vertical range was located at mean tide level. This width has been frequently used in investigations of local communities in rocky intertidal shores (e.g., Menge, 1976; Navarrete, 1996). The proportion of tidal range covered by the 100 cm plots is 72.4% (vertical extent of 138.2 cm between the



**Fig. 1.** Map of study sites. Five rocky shores (black solid squares) were chosen for the census of intertidal organisms on the Sanriku Coast (39°N, 142°E) along the Pacific coast of Japan. Five census plots (open rectangular frames) were placed on the rock wall within each shore with intervals between neighboring plots ranging from 5.7 to 348.7 m. Each census plot was vertically divided into four quadrats.

mean high water and the mean low water of spring tides). Census plots were randomly selected from among relatively steep rock slopes, and although some plots contained cracks in the rock, tide pools were absent. The angles of rock walls with respect to the verticality in the plots varied between 41° and 103° (mean  $\pm$  SD: 71.6  $\pm$  15.8°). Although the slopes varied across sites, most of the census sites (except for three plots) had slopes of between 50° and 100°, which were neither moderate nor overhanging slopes.

Intertidal benthic communities are affected by vertical environmental gradients (e.g., due to desiccation stress), and the abundance of each species varies greatly with tide levels ranging from several tens of centimeters to several meters (Bertness et al., 2006). Therefore, we divided each plot vertically into four quadrats measuring 50 cm wide by 25 cm high and surveyed the community in each quadrat.

Within each quadrat, we surveyed the abundance of 23 algal species, 20 sessile animal species, and 19 mobile mollusc species that could be identified in the field (i.e., >2 mm in length) during low tide in July 2003 (Appendix 1). All observed invertebrate species had a planktonic larval stage except for *Nucella lima*, which exhibits direct development. We counted the number of individual mobile molluscs within each quadrat. To quantify the abundance of macroalgae and sessile animals, the coverage of each species within each quadrat was determined by counting their occurrence at 50 points per quadrat (i.e., 200 points per plot) that were placed at intervals of 5 cm in both the vertical and horizontal directions. The use of coverage as estimators of species abundance is widespread in rocky shore research (e.g., Bertness et al., 2006; Lubchenco, 1980; Menge, 1976).

Nineteen environmental parameters considered to be important in influencing the community structure of rocky intertidal assemblages were measured: (1) chlorophyll *a* in sea water, (2) pheophytin in sea water, nutrients in sea water [(3) NO<sub>3</sub>, (4) NO<sub>2</sub>, (5) NH<sub>4</sub>, (6) SiO<sub>2</sub>, (7) PO<sub>4</sub>], (8) water temperature, (9) rock wall temperature, (10) tide level, (11) predator density, (12) herbivore density, (13) abundance of macroalgae, (14) abundance of sessile invertebrate, (15) disturbance frequency, (16) wave intensity, (17) orientation of rock wall, (18) rate of sediment accumulation, and (19) rock surface rugosity. Each environmental parameter was measured at a particular spatial scale based on previous reports of its spatial variability (e.g., Menge et al., 1997b). Each environmental conditions certainly vary at another spatial scale where were not measured in this study. For example, chlorophyll *a* and pheophytin in sea water could vary at finer spatial scale (e.g., among plots

within a shore). However, the variance of these environmental conditions would be large at finer scale, and then cannot be measured accurately with our methods. By contrast, some environmental conditions measured at plot and quadrat scale (e.g., wave intensity, disturbance frequency, and predator density) vary at larger spatial scale. The influence of environmental variation at larger spatial on community structure can be detected by our statistical analysis denoted in the following section. Details of the ecological importance, reference and scale of measurement of each environmental parameter are listed in Table 2, and detailed descriptions of the methods used for measuring each environmental parameter are provided in Appendix 2.

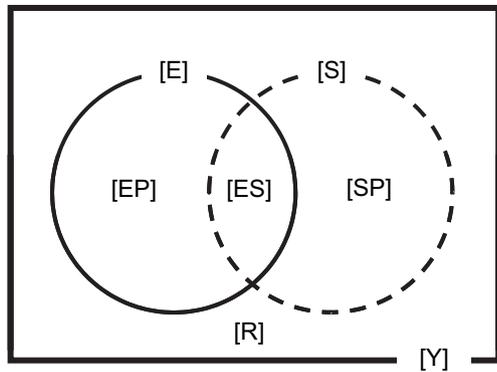
## 2.2. Statistical analysis

We conducted variation partitioning to analyze the relative contributions of environmental and spatial processes in determining community structure. This approach segregates total variation in the community matrix (i.e.,  $\beta$ -diversity) into unique environmental and spatial components with corresponding *P*-values by using the partial redundancy analysis (RDA) technique (Borcard et al., 1992; Legendre and Legendre, 1998). RDA can be best understood as a method for extending multiple regression (which has a single response and multiple predictors) to multiple response variables (several species, in this case) and a common matrix of predictors (Beisner et al., 2006). This multivariate extension of linear regression with corresponding  $r^2$  measures the percentage of the total variation in the community matrix that can be calculated from three RDAs (Fig. 2). The first RDA uses both sets of environmental and spatial variables and obtains [E + S] (i.e., [E] + [S]) indicating the total variation of the community matrix explained by environment and space. The second calculates the fraction [E] which is explained by the environmental variation involving effects of spatial variables. The third finds the fraction [S] explained by the spatial variation including effects of environmental variables. The other fractions can be obtained by simple subtraction as follows.

- (1) The fraction of variation explained by the environmental factors independent of the spatial factors:  
[EP] = [E + S] – [S]
- (2) The fraction of variation explained by spatial factors independent of environmental factors:  
[SP] = [E + S] – [E]

**Table 2**  
Environmental factors associated with ecological mechanisms that determine community structure.

Measured environmental parameter	Ecological importance	Spatial scale
Chlorophyll <i>a</i> , pheophytin	Indicators of amount of phytoplankton, which is a bottom-up effect on community structure (e.g., Bustamante et al., 1995).	Shore scale
Water temperature	Affects biomass of marine intertidal species (e.g., Ricciardi and Bourget, 1999) and species richness of intertidal organisms (e.g., Zacharias and Roff, 2001).	Shore scale
Nutrients (NO <sub>3</sub> , NO <sub>2</sub> , NH <sub>4</sub> , SiO <sub>2</sub> , PO <sub>4</sub> )	Influence community structure of rocky intertidal community through bottom-up effects (e.g., Menge et al., 1997a).	Plot scale
Disturbance frequency	Modify the degree of competitive exclusion (e.g., Dayton, 1971).	Plot scale
Temperature of rock wall	Indicator of heat stress, which is a major environmental limiting factor for intertidal organisms (e.g., Stephens and Bertness, 1991).	Plot scale
Rate of sediment accumulation	Sedimentation can negatively impact species diversity (e.g., Seapy and Littler, 1982).	Plot scale
Wave intensity	Cause physical disturbance, and moderate heat and desiccation stress (e.g., McQuaid and Branch, 1984).	Plot scale
Orientation of rock wall	The degree of wave exposure is related to the orientation of rock wall (e.g., McQuaid and Branch, 1984).	Plot scale
Predator density, herbivore density	Top down effect is important to community structure of rocky intertidal assemblages (e.g., Paine, 1974).	Quadrat scale
Abundance of macroalgae and sessile invertebrates	Abundance of macroalgae and sessile invertebrate affects intertidal herbivores (e.g., Harley, 2001) and predators (e.g., Menge, 1992), respectively.	Quadrat scale
Tide level	Tidal zonation, in which sessile species distribution depends on tidal range, is a general spatial distribution pattern in rocky intertidal assemblages (e.g., Lubchenco, 1980) and suggests that tidal level is useful as a surrogate for desiccation stress.	Quadrat scale
Rock surface rugosity	Provides refuge from predation or desiccation stress (e.g., Guichard et al., 2001).	Quadrat scale



**Fig. 2.** Venn diagram representing the fraction of the variation of response variables [Y] between two sets of predictors (environmental and spatial predictors). The rectangle represents 100% of the variation in [Y]. The total variation in [Y] is partitioned into fractions as follows: (1) fraction [E] explained by environmental predictors (solid circle); (2) fraction [S] explained by spatial predictors (dashed circle); (3) fraction [E + S] ([E] + [S]) explained by both sets of predictors (the area covered by both circles); (4) the unique fraction of variation explained by environmental predictors,  $[E_p] = [E + S] - [S]$ ; (5) the unique fraction of variation explained by spatial predictors,  $[S_p] = [E + S] - [E]$ ; (6) the common fraction of variation shared by environmental and spatial predictors,  $[ES] = [E + S] - [E_p] - [S_p]$ ; (7) the residual fraction of variation not explained by environmental and spatial predictors,  $[R] = 1 - [E + S]$ .

- (3) The fraction of variation explained by correlations between environmental and spatial factors:  
 $[ES] = [E] + [S] - [E + S]$
- (4) The residual fraction of the variation:  
 $[R] = 1 - [E + S]$

[EP] and [SP] indicate the independent effects of observed environmental conditions (associated with niche explanations) and spatial arrangement (here used to represent local dispersal processes) in determining the variation of community structure (i.e.,  $\beta$ -diversity), respectively. Hereafter, these independent effects of explanatory variables are termed as “pure effects”, which are pure not in general sense but with respect to observed environmental parameters or spatial arrangements. For example, the pure spatial effects may include some environmental factors which have not been considered in this study. [ES] represents the fraction explained by variables that cannot statistically divide environmental factors from spatial factors. [R] is the unexplained variation of community structure and includes the effects of unmeasured environmental factors and stochastic mechanisms that determine  $\beta$ -diversity.

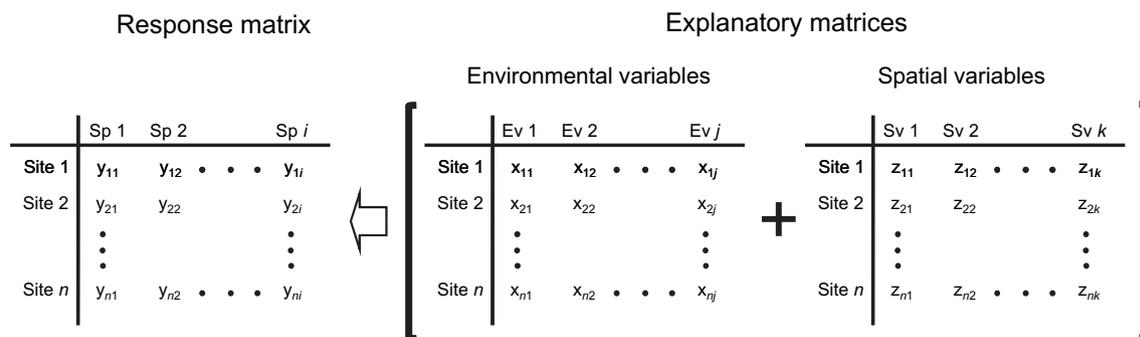
Response and explanatory variables were obtained from the abundance of each species, environmental parameters, and spatial coordinates of each quadrat (Fig. 3). As response variables, the three

community matrices were generated based on the coverage of macroalgae and sessile animals and the number of individual of mobile molluscs, which were surveyed at 100 quadrats. In the response matrix, each row shows the community structure within a quadrat (Fig. 3). Thus, the degree of variation among rows (i.e., among quadrats) indicates  $\beta$ -diversity among quadrats. Prior to analysis, the Hellinger transformation (Legendre and Gallagher, 2001) was applied to the community matrices to provide unbiased estimates of the variation partitioning based on RDA (Peres-Neto et al., 2006).

The environmental matrix was obtained from environmental parameters measured at each spatial scale. Thus, environmental parameters measured at the shore scale (i.e., pheophytin and water temperature) were shared among 20 quadrats within a shore, and environmental parameters measured at plot scale (i.e., nutrients, frequency of disturbance, rock wall temperature, speed of sediment accumulation, wave intensity, and orientation of rock wall) were shared among four quadrats within a plot (Table 2). We excluded chlorophyll *a* and  $NO_3$  from the explanatory variables because they were highly correlated with pheophytin and  $NO_2$  respectively, and explained less of the variation in the community matrix than later variables.

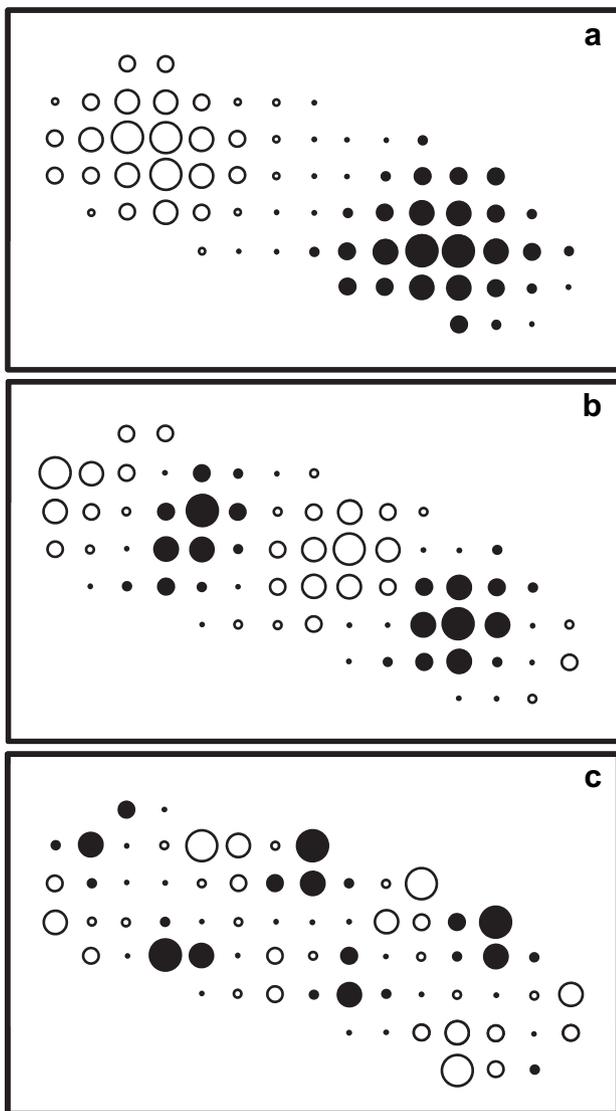
The environmental matrix represents not the environmental condition of each quadrat at the time surveying organisms but rather the environmental characteristics of each quadrat through the year. The environmental condition of a rocky intertidal zone at one specific time of the year (i.e., environmental condition at census time) may not immediately affect the community structure because of their long lifetime (for sessile animals and mobile molluscs), less mobility in the sessile stage (for macroalgae and sessile animals), and the small temporal variation of community structure (for sessile animals). The community dynamics of rocky intertidal assemblages would reflect the time lag effect of the environmental condition. Therefore, it is better to treat the environmental parameters as the environmental characteristics of each quadrat through the year, which explain the response matrices obtained from the community structure.

As spatial explanatory variables, the spatial matrix was constructed using principal coordinates of each plot; the principal coordinates of neighbor matrices (PCNM: Borcard and Legendre, 2002) were obtained for each plot. The spatial coordinates of each plot were used to obtain a Euclidean distances matrix among plot locations, then the eigenvectors associated with the positive eigenvalues of the distance matrix were used as predictor variables (henceforth, PCNM variables: Borcard and Legendre, 2002; Borcard et al., 2004). The PCNM approach has two distinct advantages over using direct geographic coordinates or trend-surface (i.e., polynomial) approaches to model spatial dependence. First, all principal coordinates are orthogonal and are therefore uncorrelated independent variables (Borcard and Legendre, 2002; Borcard et al., 2004;



**Fig. 3.** Matrices of response and explanatory variables used in variation partitioning. The response variable  $y_{ni}$  is the abundance of species *i* at study site *n* (i.e., quadrat *n*). The environmental explanatory variable  $x_{nj}$  is the parameter of environmental condition *j* at study site *n*. The spatial explanatory variable  $z_{nk}$  is the principal coordinates of neighbor matrices (PCNM) variable *k* at study site *n*. PCNM variables were obtained from the spatial coordinates of each study plot.

Dray et al., 2006); in polynomial approaches, spatial variables obviously depend on each other (e.g.,  $x$  coordinates and square of  $x$  coordinates). Second, spatial dependence can be detected over a wider range of scales (Borcard and Legendre, 2002; Borcard et al., 2004; Dray et al., 2006). Each PCNM variable has a wave-like spatial pattern: the first few PCNM variables exhibit broad-scale amplitude and frequency, and each successive variable resolves finer high-frequency, low-amplitude spatial patterns (Fig. 4; see also Borcard and Legendre, 2002; Borcard et al., 2004; Dray et al., 2006). Therefore, the results of the PCNM approach are easy to interpret and make it straightforward (compared to a polynomial approach) to detect the spatial scale in which habitat structure critically affects community structure.



**Fig. 4.** Schematic graph decomposing the geographic structure of virtual communities into PCNM variables at multiple spatial scales; (a) broad-scale, (b) middle-scale, and (c) fine-scale. Horizontal and vertical axis of each rectangle corresponds to the  $X$  (i.e., longitude) and  $Y$  coordinates (i.e., latitude) of the communities, respectively. Each bubble indicates the position of a local community plotted on the  $X$  and  $Y$  coordinates. The size of the bubble shows the absolute value of the eigenvector obtained from the principal coordinates of neighbor matrices (i.e., PCNM variable). Filled and blank bubbles show the positive and negative PCNM variables, respectively. These figures show a wave-like spatial pattern of PCNM variables. The PCNM variable of broad-scale (Fig. 4a) represents high amplitude and low frequency. By contrast, in finer spatial scale (Fig. 4c), the PCNM variable indicates low amplitude and high frequency and largely change among nearby local communities.

For each study plot, nine PCNM variables were obtained from the geographic coordinates of each plot using the statistical software R (R-Development-Core-Team, 2008) with the package “spacemaker” (Dray, 2006). The number of PCNM variables obtained from spacemaker varies depends on the spatial structure of local communities. In this study, we arbitrarily refer to PCNM variables 1–4 as shore-scale spatial structures within a region, and variables 5–9 as plot-scale spatial arrangements within a region. The four quadrats within a plot shared the same set of PCNM variables (PCNM 1–9) as well as the same set of environmental parameters measured at each plot.

Results of variation partitioning were based on the adjusted fraction of variation (Peres-Neto et al., 2006), which is analogous to adjusted  $r^2$  in multiple regression (Beisner et al., 2006). Significance of fractions was tested by permutation tests using 999 randomizations (Borcard et al., 1992).

We computed the pure relative contribution (percentage of total variation) of each pure environmental and spatial parameter in determining  $\beta$ -diversity. The pure relative contribution of each environmental parameter was obtained from a partial RDA that excluded the effect of spatial arrangement from the community matrix. The abundance of macroalgae and sessile invertebrates were respectively treated as explanation variables of community structure in order to test the dependency between macroalgae and sessile invertebrates, which could be derived from the upper limit of coverage within a quadrat. Some explanation variables were excluded from each partial RDA: abundance of macroalgae for algal species, density of herbivores and abundance of sessile invertebrates for sessile animals, and density of predators and herbivores for mobile molluscs. These explanation variables were identical to response variables or had no plausible mechanism in determining community structure. The pure relative contribution of each PCNM variable was acquired by a partial RDA that excluded effects of environmental parameters from the community matrix.

The variation partitioning, permutation test, and partial RDA were carried out using the statistical software R (R-Development-Core-Team, 2008) with the add-on package “vegan” (Oksanen et al., 2008).

### 3. Results

#### 3.1. Variation partitioning

Both environmental and spatial predictors significantly explained  $\beta$ -diversity for each taxonomic group (Table 3). Predictor variables explained 29.7–50.8% of the total variation in abundance of each species (macroalgae, 50.8%; sessile animals, 45.7%; and mobile molluscs, 29.7%). The relative contribution of environmental predictors in determining  $\beta$ -diversity was larger than that of spatial predictors in all taxonomic groups (Table 3). Pure environmental predictors explained 16.7–40.7% of total variation (macroalgae, 29.3%; sessile animals 40.7%; and mobile molluscs, 16.7%), and pure spatial predictors explained another 3.6–19.9% of total variation (macroalgae, 19.9%; sessile animals, 3.6%; and mobile molluscs, 6.6%).

#### 3.2. Partial RDA

Results of partial RDA excluding the effect of spatial arrangement indicated that each pure environmental parameter explained a small fraction (<8%) of the total variation of community structure (mean  $\pm$  SD:  $1.37 \pm 1.37$ ; Table 4). Pheophytin (3–5%) and tide level (1–8%) significantly explained  $\beta$ -diversity in all taxonomic groups. For sessile animals, tide level showed a high fraction of explained variation (8%).

Results of partial RDA excluding the effect of environmental conditions showed that PCNM variables explained a small fraction (<3%) of the total variation of community structure (mean  $\pm$  SD:

**Table 3**

Results of variation partitioning of community abundance for three taxonomic groups. The adjusted  $r^2$  with associated  $p$ -values are presented. [EP] is the pure effect of environmental factors, [SP] is the pure effect of spatial factors, [ES] is the overlap between environmental and spatial predictors, and [R] is the residual variation of total variance of the community matrix. In this analysis, negative values of adjusted  $r^2$  were treated as 0.

Variables	Macroalgae		Sessile animals		Mobile molluscs	
	Adj. $r^2$	$p$	Adj. $r^2$	$p$	Adj. $r^2$	$p$
[EP]	0.293	0.001	0.407	0.001	0.167	0.001
[SP]	0.199	0.001	0.036	0.009	0.066	0.001
[ES]	–0.041		0.015		0.063	
[R]	0.550		0.543		0.703	

1.08 ± 0.79; Table 5). Broader spatial structure (i.e., shore scale, as represented by PCNM variables 1–4) explained  $\beta$ -diversity significantly or marginally significantly in all taxonomic groups (except for PCNM 3 in macroalgae; PCNM 3, 4 in sessile animals; and PCNM 1 in mobile molluscs). At plot scale (represented by PCNM variables 5–9), spatial structure significantly explained  $\beta$ -diversity for algal community (PCNM 7, 1%; PCNM 8, 3%; and PCNM 9, 1%). However, plot-scale structure did not explain  $\beta$ -diversity for sessile animals and mobile molluscs (except for the marginal significance of PCNM 5, 6 in sessile animals and a PCNM 5 significance of  $P = 0.037$  in mobile molluscs).

#### 4. Discussion

The results of variation partitioning indicated that the variation of community structure (i.e.,  $\beta$ -diversity) was explained better by environmental predictors than by spatial predictors, suggesting that environmental processes associated with niche explanations were more important than spatial processes, which may be related to dispersal processes in determining community structure. The results of this study confirm findings of previous studies in which species interaction and related environmental conditions were reported to play a key role in structuring rocky intertidal assemblages at the patch scale (e.g., Connell, 1961; Menge and Branch, 2001; Paine, 1966).

The fraction of  $\beta$ -diversity explained by pure spatial predictors was greater for macroalgae than for sessile animals and mobile molluscs. These results suggest that even if taxonomic groups live

**Table 4**

Portion of variation explained by each pure environmental variable obtained by partial redundancy analysis (RDA). “–” indicated explanation variables that were excluded from each partial RDA. Scales of measurement for each variable are listed in Table 1.

Variables	Macroalgae		Sessile animals		Mobile molluscs	
	%	$p$	%	$p$	%	$p$
Shore scale						
Pheophytin	5	<0.001	4	<0.001	3	<0.001
Water temperature	0.2	0.627	2	0.001	1	0.008
Plot scale						
NO <sub>2</sub>	1	0.031	1	0.061	1	0.100
NH <sub>4</sub>	1	0.049	1	0.012	1	0.148
PO <sub>4</sub>	1	0.020	0.4	0.240	1	0.174
SiO <sub>2</sub>	1	0.003	0.5	0.204	0.4	0.390
Disturbance	1	0.001	1	0.034	0.2	0.776
Rock temperature	1	0.023	1	0.012	1	0.084
Sediment	1	0.012	2	<0.001	1	0.136
Wave intensity	1	0.009	0.1	0.847	1	0.072
Orientation	2	0.001	1	0.130	1	0.013
Quadrat scale						
Predators	0.5	0.126	3	<0.001	–	–
Herbivores	1	0.004	–	–	–	–
Macroalgae	–	–	2	<0.001	1	0.016
Sessile invertebrates	1	0.066	–	–	1	0.012
Tide level	1	0.011	8	<0.001	2	<0.001
Rugosity	0.4	0.128	1	0.089	0.4	0.268

**Table 5**

Portion of variation explained by each pure principal coordinates of neighbor matrices (PCNM) variable obtained by partial redundancy analysis (RDA).

Variables	Macroalgae		Sessile animals		Mobile molluscs	
	%	$p$	%	$p$	%	$p$
PCNM 1	1	<0.001	1	0.010	0.2	0.827
PCNM 2	3	<0.001	1	0.096	1	0.001
PCNM 3	0.4	0.184	0.4	0.331	1	0.018
PCNM 4	1	0.008	0.3	0.442	1	0.008
PCNM 5	0.2	0.471	1	0.052	1	0.037
PCNM 6	0.3	0.333	1	0.059	1	0.104
PCNM 7	1	0.006	0.2	0.695	1	0.155
PCNM 8	3	<0.001	0.3	0.476	1	0.106
PCNM 9	1	0.017	0.4	0.318	1	0.163

in the same ecosystem, share common resources, and interact with each other, they have different determinant mechanisms of community structure that depend on ecological characteristics such as dispersal ability and life history. Likewise, previous studies of lake communities have shown that community structures of organisms with lower dispersal are better explained by spatial structures than are community structure of taxa with greater dispersal (Beisner et al., 2006; Soininen et al., 2007).

Three mechanisms related to ecological characteristics may cause the differences in the relative contributions of spatial processes among taxonomic groups observed in the present study. The first mechanism is the difference in dispersal distance between macroalgal propagules and invertebrate larvae. We cannot compare dispersal ability among the taxonomic groups observed in this study because there has been little research reporting dispersal abilities of these organisms. However, Kinlan and Gaines (2003) indicated that herbivores and competitors of macroalgae (i.e., sessile invertebrates) may disperse from one to five orders of magnitude further than the algae with which they interact. Dispersal distances of marine invertebrate larvae have been shown to range from several tens of centimeters to several hundreds of kilometers (Kinlan and Gaines, 2003). Therefore, species with great dispersal ability may be able to reach every habitat within the distances of pairs of plots (ranging from 5.7 to 348.7 m) and of shores (ranging from 4.1 to 25.7 km). Accordingly, post-settlement processes dependent on the environmental conditions of each habitat may become more important in determining  $\beta$ -diversity than dispersal limitations. Meanwhile, dispersal distances of algal propagules were found to range from several tens of centimeters to several tens of kilometers (Kendrick and Walker, 1991; Kinlan and Gaines, 2003). Therefore, even macroalgal species with high dispersal ability would have some difficulty in reaching suitable habitats, and the relative importance of dispersal limitation on community structure for macroalgae would be greater than for marine invertebrates.

The second mechanism is the ability of marine invertebrate larvae to select a settlement substrate. Larvae can selectively settle on suitable habitat guided by abiotic cues (e.g., Crisp, 1978; Meadows and Campbell, 1972; Pawlik and Butman, 1993; Tambutti et al., 1992) or the presence of conspecifics that are indicative of suitable habitat (e.g., Jeffery, 2000; Minchinton, 1997; Raimondi, 1988, 1991). Therefore, the spatial structure of the invertebrate community would be affected more by environmental heterogeneity, especially environmental conditions at a smaller scale where larva can actively move in their planktonic stage, than by spatial distances among local communities. On the other hand, a few types of macroalgal propagules have the ability to actively select specific settlement sites (e.g., Johnson, 1994). Thus, such macroalgae may experience a larger relative contribution of recruitment processes, resulting in community variation as explained by spatial factors.

Lastly, the life history of each organism presumably affects the differences in relative contribution of environmental and spatial processes among taxonomic groups. A species with a longer lifespan is exposed to post-recruitment processes for a longer duration. The post-recruitment processes may be mainly caused by environmental factors and are thus important for organisms with a long lifespan. In contrast, species with shorter lifespans experience a more dominant contribution of pre-recruitment processes in determining their population dynamics. The pre-recruitment processes would be mainly caused by spatial factors, which act more importantly on organisms with a shorter lifespan. To our knowledge, there have been few studies that have reported lifespans of the organisms observed in this study. Furthermore, some macroalgae and sessile invertebrates undergo two modes of reproduction; i.e., clonal propagation and broadcasting of dispersal propagules (spores and larvae). Therefore, it is difficult to conduct concrete a discussion about the influence of lifespan on the relative contribution of environmental and spatial processes in determining community structure.

Like as other analytical methods, variation partitioning has some drawbacks. First, it is difficult to quantify all the environmental factors related to the niche explanation, and thus we cannot accurately evaluate the influence of environmental conditions which are not measured. In the results of variation partitioning, the influence of these environmental conditions is involved in the fraction of spatial factors or the residual (unexplained) fraction. Second, variation partitioning cannot directly test the influence of interaction among environmental factors. In rocky intertidal assemblages, previous studies show the important role of the interaction among environmental factors in determining community structure (e.g., Bertness et al., 1999; Menge and Sutherland, 1987). However, these unquantified uncertainties may not degrade the main conclusion based on the results of variation partitioning. If these uncertainties were eliminated, the relative contribution of environmental factors could be greater, and then our conclusion would be robust.

The fraction of  $\beta$ -diversity explained by pure environmental variables for mobile molluscs was smaller than for sessile animals. This difference is probably caused by the fact that some mobile molluscs do not always stay within a plot. Mobile molluscs may be affected by environmental conditions at a larger grain size than our census plot, whereupon the effects of environmental factors specific to the plot and quadrat on mobile molluscs may be weaker than on sessile invertebrate. This is supported by the results of partial RDA (Table 4).

Although  $\beta$ -diversity was explained by pheophytin and tide level for all taxonomic groups, other environmental parameters significantly explaining  $\beta$ -diversity differed among taxonomic group (Table 4). This suggests that important niche axes (i.e., key environmental factors) in determining community structure differ among taxonomic groups even if the groups live in the same ecosystem. To our knowledge, this has not been directly examined in rocky intertidal assemblages. However, previous studies provide indirect support for this concept. For example, Wootton et al. (1996) showed the influence of nutrient addition on abundance differences between macroalgae and herbivores.

The importance of scale in spatial arrangement of local communities for determining community structure differed among taxonomic groups (Table 5). For sessile animals and mobile molluscs,  $\beta$ -diversity was significantly explained by spatial structure only at shore scale, while variations in algal communities were significantly explained by spatial structure at both the shore and plot scale. This result suggests that spatial processes, especially dispersal limitation, in determining community structure differ among taxonomic groups depending on ecological characteristics such as dispersal ability. A similar result was reported by Nakaoka et al. (2006) from the Pacific coast of Japan (including the region studied here). Distance-decay of community similarity among plots was greatest

for algae, but distance-decay of community similarity among shores was greatest for sessile animals. This fact indicates that when we conduct a study dealing with community dynamics in the open system, we should pay attention to the spatial extent of communities corresponding to the dispersal ability of focusing taxonomic groups.

We have to notice the limitations of the analytical approach in the interpretation of the results. Results obtained by variation partitioning could not translate clearly into an understanding of what metacommunity processes are important for spatial patterns of community structure. Because metacommunity processes in marine benthic communities (including our rocky intertidal assemblages) are likely to be considerably more complicated than the processes usually discussed under the metacommunity framework. In particular, the dispersal processes for marine invertebrate with planktonic larvae are thought to be driven by complex oceanographic processes (e.g., Connolly and Roughgarden, 1998; Menge et al., 2004; Noda, 2004). The analysis of spatial pattern of community structure essentially assumes that if communities which are closer to each other are more similar and if this similarity is not accounted for by environmental variables, and then the spatial pattern of community structure is due to dispersal limitation. This distance-decay of community similarity is used as evidences of patch dynamics model and/or neutral model on metacommunity dynamics contrasting to species sorting model which assumed that pure environmental processes are main driver of metacommunity dynamics (e.g., Cottenie, 2005). However, for marine invertebrate communities, larvae dispersal itself may be affected by environmental condition as already mentioned. As a result, if environmental variables are successful predictors of community composition, environmental explained variation of community could reflect not only environmental processes in benthic stage but also environmental processes in planktonic stage, which are hardly distinguished from spatially dispersal processes.

## 5. Conclusion

We have examined the relative contribution of environmental processes (related to niche explanation) and spatial processes (associated with dispersal) in determining community structure for all major taxonomic groups in a specific ecosystem type. In the rocky intertidal shores along the Sanriku Coast of Japan, community structure is under the greater influence of spatial processes for macroalgae than for marine invertebrates (i.e., sessile animals and mobile molluscs). Although some taxonomic groups live in the same ecosystem, it was likely that the mechanisms that determined their community structure changed depending on ecological characteristics such as dispersal ability and life history. An in-depth study concerning variability of the dependence of key niche axes on ecological characteristics associated with taxonomic groups, such as dispersal ability, resistance to environmental stress, and biological interaction, would provide great insights into understanding the general rules of the complex mechanisms that structure communities. This knowledge would contribute to the ability to predict the ecological impact of global warming and to conserve the biodiversity threatened by human activity.

## Acknowledgments

For field and laboratory facilities, we are grateful to the staff and students of the International Coastal Research Center of the Ocean Research Institute, The University of Tokyo. This study was made possible by the generous support and encouragement of local fishermen and the offices of the Fisherman's Cooperative Associations in Iwate Prefecture. We thank Y. Fukatsu, N. Ito, T. Maruyama, M. Tsujino, A. Aizawa, M. Takahata, and many others for their help with our fieldwork and data analyses; N. Kouchi for taxonomic

identification of the intertidal sessile animals; and Dr. D. Munroe for critically reading and checking the English text. This research was supported by a grant-in-aid from the Ministry of Education, Science, Culture and Sports, Japan (No. 14340242).

## Appendix 1

List of macroalgae, sessile animals, and mobile molluscs observed in this study.

Taxonomic group	Class	Order	Species		
Macroalgae	Chlorophyceae	Cladophorales	<i>Cladophora</i> spp.		
		Ulvales	<i>Ulva pertusa</i>		
	Phaeophyceae	Chordariales	<i>Pterospongium rugosum</i>		
		Fucales	<i>Sargassum fusiformis</i> <i>Sargassum thunbergii</i>		
	Rhodophyceae	Ralfsiales	<i>Analipus japonicus</i> <i>Endoplura aurea</i> <i>Ralfsiales</i> spp.		
		Ceramiales	<i>Chondria crassicaulis</i> <i>Laurencia okamurae</i>		
			Corallinales	<i>Corallina pilulifera</i> <i>Corallinaceae</i> spp.	
		Gelidiales	<i>Gelidium divaricatum</i> <i>Pterocladia tenuis</i>		
		Gigartinales	<i>Carpopeltis affinis</i> <i>Chondracanthus intermedius</i> <i>Chondrus elatus</i> <i>Chondrus yendoi</i> <i>Chondrus</i> spp.		
			Hildenbrandiales	<i>Gloiopeltis furcata</i> <i>Peyssonelia conchicola</i> <i>Hildenbrandia rubra</i> <i>Cyanophyceae</i> spp.	
				Cyanophyceae	
		Sessile animals	Bivalvia	Arcoidea	<i>Arca boucardi</i>
				Ostreoida	<i>Crassostrea gigas</i>
				Mytiloida	<i>Mytilus galloprovincialis</i> <i>Mytilus coruscus</i>
	Bryozoa		Cheilostomata	<i>Watersipora suboboidea</i> <i>Microporella orientalis</i> <i>Cheilostomata</i> sp.	
				<i>Capitulum mitella</i> <i>Semibalanus cariosus</i> <i>Semibalanus grandulata</i> <i>Chthamalus challengerii</i>	
	Cirripedia		Pedunculata	<i>Pyura vittata</i>	
				<i>Anthopleura japonica</i> <i>Anthopleura fuscoviridis</i> <i>Actinia equina</i>	
	Ascidiacea		Pleurogona	<i>Anthopleura japonica</i> <i>Anthopleura fuscoviridis</i> <i>Actinia equina</i>	
Actiniaria				<i>Anthopleura japonica</i> <i>Anthopleura fuscoviridis</i> <i>Actinia equina</i>	
Hydrozoa	Leptomedusae		<i>Leptomedusae</i> sp.		
			<i>Sabellastarte japonica</i> <i>Hydroides ezoensis</i>		
Polychaeta	Sabellida		<i>Sabellastarte japonica</i> <i>Hydroides ezoensis</i>		
		<i>Halichondria japonica</i> <i>Haliclona permollis</i>			
Mobile molluscs	Gastropoda	Archaeogastropoda	<i>Gastropoda</i> sp. <i>Cellana grata</i> <i>Cellana toreuma</i> <i>Chlorostoma lischkei</i> <i>Lottia kogamogai</i> <i>Lottia lindbergi</i> <i>Lottia tenuisculpta</i> <i>Monodonta labio</i> <i>Monodonta neritoides</i> <i>Nipponacmea concinna</i> <i>Nipponacmea fuscoviridis</i> <i>Nipponacmea schrenckii</i>		
		Mesogastropoda	<i>Littorina brevicula</i> <i>Nodilittorina radiata</i>		
		Neogastropoda	<i>Nucella lima</i> <i>Thais clavigera</i>		
		Polyplacophora	Neoloricata	<i>Acanthochitona achates</i> <i>Acanthopleura japonica</i>	
			Pulmonata	<i>Siphonaria japonica</i>	

## Appendix 2. Methods of measurement for each environmental factor.

### Chlorophyll *a* and pheophytin

To measure chlorophyll *a* and pheophytin, 114 ml sea water at the surface with a polyethylene bottle at each shore in summer (July and August 2003), early winter (November and December 2003), and spring (April and May 2004). To prevent zooplankton feeding on phytoplankton, sea water was suction filtered through a glass fibre filter (25- $\mu$ m pore size: GF/F, GE Healthcare UK Ltd, Little Chalfont, Buckinghamshire, England) under 0.2 atm using a manual vacuum pump (HP-01, Toyo Roshi, Tokyo, Japan) at the time of sampling. The filtered glass fibre filter was soused in *N,N*-dimethylformamide (DMF) to extract chlorophyll *a* and pheophytin. After extraction, the DMF and filter were frozen at  $-20^{\circ}\text{C}$  until analysis of chlorophyll *a* and pheophytin. Extracted samples were quantified using a fluorometer (Fluorometer AU 10-005, Turner Designs, Sunnyvale, California, USA). The annual average of measured values was used as the value of chlorophyll *a* and pheophytin at each shore.

### Nutrients

To measure nutrients, 100 ml sea water was sampled using a polyethylene bottle at each plot in parallel with measuring of chlorophyll *a* and pheophytin. Before sampling sea water, we washed the polyethylene bottles with hydrochloric acid and distilled water. Bottles containing sea water were frozen at  $-20^{\circ}\text{C}$  until nutrient analysis. After defrosting,  $\text{NO}_3$ ,  $\text{NO}_2$ ,  $\text{NH}_4$ ,  $\text{SiO}_2$ , and  $\text{PO}_4$  were quantified by an automated chemical-analyzer (AACS4, BL TEC, Osaka, Japan). The annual average of measured values was used as the value of  $\text{NO}_3$ ,  $\text{NO}_2$ ,  $\text{NH}_4$ ,  $\text{SiO}_2$ , and  $\text{PO}_4$  at each plot.

### Temperature

Surface water temperature was measured using a digital thermometer (CT-220, Custom, Tokyo, Japan) at each shore in summer (July and August 2003), early winter (November and December 2003), and spring (April and May 2004). The annual average of measured values was used as the value of water temperature at each shore.

To measure annual highest temperature of each rock wall, a thermo logger (StowAway Tidbit, Onset Computer Corp., Bourne, Massachusetts, USA) was embedded in the dug rock surface of selected plots at the mean tidal level using epoxy putty (Splash Zone compound E380, Konishi, Osaka, Japan). Each logger recorded average temperature every 6 min. The rock temperature measurements were conducted from July to November 2006. Because the logger was embedded at only one plot within a shore, we estimated the highest rock temperature at another four plots within a shore using measured rock temperature (Shiraishi & Nakaoka, unpublished data). Rock surface temperature was measured at all study plots using a radiation thermometer (IT-540NH, Horiba, Kyoto, Japan) between July and September 2006 (the most thermally stressful season). To estimate highest rock temperature at plots without loggers, we conducted multiple regression using temperature measured by radiation thermometer and logged highest temperature. Both measured and estimated highest temperatures were used as the value of the temperature of rock wall at each plot.

### Tide level

We recorded the midpoint height of each quadrat relative to standard sea level in Japan.

### Density of predator and herbivore.

To quantify the number of carnivorous and phytophagous invertebrates (except crustaceans), the number of carnivorous and phytophagous mobile molluscs was counted at each quadrat.

### Amount of food supply

Abundance of macroalgae and sessile invertebrates were quantified by using coverage data of them at each quadrat.

### Frequency of disturbance

Frequency of disturbance was obtained based on the transition of organisms at each plot. In April and May 2003 and July and August 2003, we recorded the presence or absence of all sessile organisms at 200 fixed grid points per plot, which were permanently marked with plastic or stainless steel anchors. We calculated the mortality rate of each plot using the number of grid points that changed from presence of some organism to absence of any organisms. We used this mortality rate as the parameter of frequency of disturbance.

### Wave intensity

Maximum wave intensity during each month from May 2003 to July 2004 was measured by a maximum velocity recorder (Bell and Denny, 1994). Average maximum wave intensity was used as the value of wave intensity at each plot.

### Rate of sediment accumulation

Sediment accumulation was measured with plastic chip sediment traps (101–1000 µl Pipet Tip, Quality Scientific Plastics, Petaluma, California, USA) deployed in mean tide level at each plot from July 2003 to June 2004. To trap sediment in the chip, the front edge of the chip was melted and closed. Sediment traps were deployed for 1 month; at high-sedimentation locations deployment time was decreased. We divided the amount of sediment by accumulation time to calculate daily sedimentation rate. The annual average of sediment per day was used as the rate of sediment accumulation at each plot.

### Physiographical features

The orientation of the rock surface (aspect) was used as orientation of rock wall in each plot. Rugosity of rock surface topography was obtained by calculating the ratio between linear distance of the rock surface and distance along the surface of the rock wall using a pattern recording gauge (Katatori-gauge, Shinwa-sokutei, Niigata, Japan) at each quadrat.

## References

- Beisner, B.E., Peres, P.R., Lindstrom, E.S., Barnett, A., Longhi, M.L., 2006. The role of environmental and spatial processes in structuring lake communities from bacteria to fish. *Ecology* 87, 2985–2991.
- Bell, E.C., Denny, M.W., 1994. Quantifying “wave exposure”: a simple device for recording maximum velocity and results of its use at several field sites. *J. Exp. Mar. Biol. Ecol.* 181, 9–29.
- Bertness, M.D., Leonard, G.H., Levine, J.M., Bruno, J.F., 1999. Climate-driven interactions among rocky intertidal organisms caught between a rock and a hot place. *Oecologia* 120, 446–450.
- Bertness, M.D., Crain, C.M., Silliman, B.R., Bazterrica, M.C., Reyna, M.V., Hildago, F., Farina, J.K., 2006. The community structure of Western Atlantic Patagonian rocky shores. *Ecol. Monogr.* 76, 439–460.
- Borcard, D., Legendre, P., 2002. All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecol. Modell.* 153, 51–68.
- Borcard, D., Legendre, P., Drapeau, P., 1992. Partialling out the spatial component of ecological variation. *Ecology* 73, 1045–1055.
- Borcard, D., Legendre, P., Avois-Jacquet, C., Tuomisto, H., 2004. Dissecting the spatial structure of ecological data at multiple scales. *Ecology* 85, 1826–1832.
- Bustamante, R.H., Branch, G.M., Eekhout, S., Robertson, B., Zoutendyk, P., Schleyer, M., Dye, A., Hanekom, N., Keats, D., Jurd, M., McQuaid, C., 1995. Gradients of intertidal primary productivity around the coast of South-Africa and their relationships with consumer biomass. *Oecologia* 102, 189–201.
- Connell, J.H., 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus Stellatus*. *Ecology* 42, 710–723.
- Connolly, S.R., Roughgarden, J., 1998. A latitudinal gradient in Northeast Pacific intertidal community structure: evidence for an oceanographically based synthesis of marine community theory. *Am. Nat.* 151, 311–326.
- Cottenie, K., 2005. Integrating environmental and spatial processes in ecological community dynamics. *Ecol. Lett.* 8, 1175–1182.
- Crisp, D.J., 1978. Genetic consequences of different reproductive strategies in marine invertebrates. In: Battaglia, B., Beardmore, J.A. (Eds.), *Marine Organisms: Genetics, Ecology and Evolution*. Plenum Press, New York, USA, pp. 257–273.
- Dayton, P.K., 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecol. Monogr.* 41, 351–389.
- Dray, S., Legendre, P., Peres-Neto, P.R., 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecol. Modell.* 196, 483–493.
- Dray, S., 2006. Spacemaker: spatial modelling, version 0.0-2. <http://biomserv.univ-lypn.fr/~dray/>.
- Guichard, F., Bourget, E., Robert, J.L., 2001. Scaling the influence of topographic heterogeneity on intertidal benthic communities: alternate trajectories mediated by hydrodynamics and shading. *Mar. Ecol. Prog. Ser.* 217, 27–41.
- Harley, C.D.G., 2001. Light availability indirectly limits herbivore growth and abundance in a high rocky intertidal community during the winter. *Limnol. Oceanogr.* 47, 1217–1222.
- Holyoak, M., Leibold, M.A., Monquet, N.M., Holt, R.D., Hoopes, M.F., 2005. Metacommunities: a framework for large-scale community ecology. In: Holyoak, M., Leibold, M.A., Holt, R.D. (Eds.), *Metacommunities. Spatial Dynamics and Ecological Communities*. The University of Chicago Press, Chicago, Illinois, USA, pp. 1–31.
- Jeffery, C.J., 2000. Settlement in different-sized patches by the gregarious intertidal barnacle *Chamaesipho tasmanica* Foster and Anderson in New South Wales. *J. Exp. Mar. Biol. Ecol.* 252, 15–26.
- Johnson, L.E., 1994. Enhanced settlement on microtopographical high points by the intertidal red alga *Halosaccion glandiforme*. *Limnol. Oceanogr.* 39, 1893–1902.
- Kearney, M., 2006. Habitat, environment and niche: what are we modelling? *Oikos* 115, 186–191.
- Kendrick, G.A., Walker, D.I., 1991. Dispersal distances for propagules of *Sargassum spinuligerum* (Sargassaceae, Phaeophyta) measured directly by vital staining and venturi suction sampling. *Mar. Ecol. Prog. Ser.* 79, 133–138.
- Kinlan, B.P., Gaines, S.D., 2003. Propagule dispersal in marine and terrestrial environments: a community perspective. *Ecology* 84, 2007–2020.
- Legendre, P., Gallagher, E.D., 2001. Ecologically meaningful transformations for ordination of species data. *Oecologia* 129, 271–280.
- Legendre, P., Legendre, L., 1998. *Numerical Ecology*, second ed. Elsevier Science B.V., Amsterdam, The Netherlands.
- Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M., Gonzalez, A., 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecol. Lett.* 7, 601–613.
- Lubchenco, J., 1980. Algal zonation in the New England rocky intertidal community: an experimental analysis. *Ecology* 61, 333–344.
- McGill, B.J., Enquist, B.J., Weiher, E., Westoby, M., 2006. Rebuilding community ecology from functional traits. *Trends Ecol. Evol.* 21, 178–185.
- McQuaid, C.D., Branch, G.M., 1984. Influence of sea temperature, substratum and wave exposure on rocky intertidal communities – an analysis of faunal and floral biomass. *Mar. Ecol. Prog. Ser.* 19, 145–151.
- Meadows, P.S., Campbell, J.L., 1972. Habitat selection by aquatic invertebrates. *Adv. Mar. Biol.* 10, 271–382.
- Menge, B.A., Branch, G.M., 2001. Rocky intertidal communities. In: Bertness, M.D., Gaines, S.D., Hay, M.E. (Eds.), *Marine Community Ecology*. Sinauer Associates, Sunderland, Massachusetts, USA, pp. 221–251.
- Menge, B.A., Sutherland, J.P., 1987. Community regulation – variation in disturbance, competition, and predation in relation to environmental-stress and recruitment. *Am. Nat.* 130, 730–757.
- Menge, B.A., Daley, B.A., Wheeler, P.A., Dahlhoff, E., Sanford, E., Strub, P.T., 1997a. Benthic-pelagic links and rocky intertidal communities: bottom-up effects on top-down control? *Proc. Natl. Acad. Sci. U.S.A.* 94, 14530–14535.
- Menge, B.A., Daley, B.A., Wheeler, P.A., Strub, P.T., 1997b. Rocky intertidal oceanography: an association between community structure and nearshore phytoplankton concentration. *Limnol. Oceanogr.* 42, 57–66.
- Menge, B.A., Blanchette, C., Raimondi, P., Freidenburg, T., Gaines, S., Lubchenco, J., Lohse, D., Hudson, G., Foley, M., Pamplin, J., 2004. Species interaction strength: testing model predictions along an upwelling gradient. *Ecol. Monogr.* 74, 663–684.
- Menge, B.A., 1976. Organization of the New England rocky intertidal community: role of predation, competition and environmental heterogeneity. *Ecol. Monogr.* 46, 355–393.
- Menge, B.A., 1992. Community regulation: under what conditions are bottom-up factors important on rocky shores? *Ecology* 73, 755–765.
- Menge, B.A., 1995. Indirect effects in marine rocky intertidal interaction webs – patterns and importance. *Ecol. Monogr.* 65, 21–74.

- Minchinton, T.E., 1997. Life on the edge: conspecific attraction and recruitment of populations to disturbed habitats. *Oecologia* 111, 45–52.
- Nakaoka, M., Ito, N., Yamamoto, T., Okuda, T., Noda, T., 2006. Similarity of rocky intertidal assemblages along the Pacific coast of Japan: effects of spatial scales and geographic distance. *Ecol. Res.* 21, 425–435.
- Navarrete, S.A., 1996. Variable predation: effects of whelks on a mid-intertidal successional community. *Ecol. Monogr.* 66, 301–321.
- Noda, T., 2004. Large-scale variability in recruitment of the barnacle *Semibalanus cariosus*: its cause and effects on the population density and predator. *Mar. Ecol. Prog. Ser.* 278, 241–252.
- Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Simpson, G.L., Stevens, M.H.H., 2008. *vegan: community ecology package, version 1.13-0.* <http://cran.r-project.org/>.
- Paine, R.T., 1966. Food web complexity and species diversity. *Am. Nat.* 100, 65–75.
- Paine, R.T., 1974. Intertidal community structure. *Oecologia* 15, 93–120.
- Pawlik, J.R., Butman, C.A., 1993. Settlement of a marine tube worm as a function of current velocity: interacting effects of hydrodynamics and behavior. *Limnol. Oceanogr.* 38, 1730–1740.
- Peres-Neto, P.R., Legendre, P., Dray, S., Borcard, D., 2006. Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology* 87, 2614–2625.
- Raimondi, P.T., 1988. Settlement cues and determination of the vertical limit of an intertidal barnacle. *Ecology* 69, 400–407.
- Raimondi, P.T., 1991. Settlement behavior of *Chthamalus anisopoma* larvae largely determines the adult distribution. *Oecologia* 85, 349–360.
- R-Development-Core-Team, 2008. R: a Language and Environment for Statistical Computing, Ver. 2.7.0. R Foundation for Statistical Computing, Vienna, Austria. <http://cran.r-project.org/>.
- Ricciardi, A., Bourget, E., 1999. Global patterns of macroinvertebrate biomass in marine intertidal communities. *Mar. Ecol. Prog. Ser.* 185, 21–35.
- Seapy, R.R., Littler, M.M., 1982. Population and species diversity fluctuations in a rocky intertidal community relative to severe aerial exposure and sediment burial. *Mar. Biol.* 71, 87–96.
- Soininen, J., Kokocinski, M., Estlander, S., Kotanen, J., Heino, J., 2007. Neutrality, niches, and determinants of plankton metacommunity structure across boreal wetland ponds. *Ecoscience* 14, 146–154.
- Stephens, E.G., Bertness, M.D., 1991. Mussel facilitation of barnacle survival in a sheltered bay habitat. *J. Exp. Mar. Biol. Ecol.* 145, 33–48.
- Tambutti, M.N., Zimmer-faust, R.K., Tamplin, M.L., 1992. Natural sources and properties of chemical inducers mediating settlement of oyster larvae: a re-examination. *Biol. Bull.* 183, 327–338.
- Wilson, D.S., 1992. Complex interactions in metacommunities, with implications for biodiversity and higher levels of selection. *Ecology* 73, 1984–2000.
- Wootton, J.T., Power, M.E., Paine, R.T., Pfister, C.A., 1996. Effects of productivity, consumers, competitors, and El Niño events on food chain patterns in a rocky intertidal community. *Proc. Natl. Acad. Sci. U.S.A.* 93, 13855–13858.
- Zacharias, M.A., Roff, J.C., 2001. Explanations of patterns of intertidal diversity at regional scales. *J. Biogeogr.* 28, 471–483.