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**Similarity of rocky intertidal assemblages along the Pacific
Coast of Japan: Effects of spatial scales and geographic
distance**

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Abstract Factors and processes affecting community structures operate at various spatial and temporal scales. We analyzed how similarities of rocky intertidal assemblages vary at different spatial scales using a nested, hierarchical sampling design. Intertidal assemblages consisting of algae, sessile animals and mobile animals were censused on five rock walls at each of five shores chosen within each of six regions along the Pacific coast of Japan encompassing 1800 km coastlines. Based on this sampling design, similarities in assemblages were calculated using both qualitative (presence/absence) and quantitative (percent cover and density) data, and compared at three spatial levels; (1) rock level (the finest spatial scale: encompassing several to hundreds of meters), (2) shore level (the intermediate spatial scale: several to tens of kilometers) and (3) region level (the broadest spatial scale: hundreds to thousands of kilometers). Cluster analysis showed that assemblages were categorized into distinct regional groups except for the two southern regions, whereas they did not separate clearly from each shore. A nested ANOSIM revealed significant variation in similarities among regions, and among shores within each region, with the former showing greater variation. Similarity was negatively correlated with geographic distance at the regional level, but not at the shore and the rock levels. At the regional level, similarity decreased more rapidly with distance for mobile animals than sessile organisms. The analyses highlighted the importance of broad-scale abiotic/biotic factors such as oceanic current conditions and biogeographical factors in determining observed patterns in similarity of rocky intertidal assemblages.

Keywords Geographic distance, Hierarchical design, Marine benthic organisms, Multivariate analyses, Pacific coast of Japan

48 **Introduction**

49

50 Structures and dynamics of biological communities are influenced by numerous biotic
 51 and abiotic factors that operate at various spatial and temporal scales. In marine
 52 benthic communities, some physical and oceanographic processes such as oceanic
 53 current dynamics and climate variation affect organisms at broadest spatial scale such as
 54 hundreds to thousands of kilometers (Crisp and Southward 1958; Briggs 1995), whereas
 55 species interaction such as competition, predation and facilitation occur between
 56 adjacent individuals at finest spatial scale of centimeters (Connell 1961; Paine 1966;
 57 Bruno and Bertness 2001; Duffy and Hay 1992). At intermediate scales, patterns of
 58 larval dispersal with coastal currents can greatly affect population and community
 59 structures of benthic organisms at the scale of tens to hundreds of kilometers
 60 (Roughgarden et al. 1988; Gaines and Bertness 1992; Hyder et al. 1998; Morgan 2001;
 61 Underwood and Keough 2001). Clarification of relative importance of multiple
 62 factors operating at different scales and of their interacting effects is crucial and
 63 challenging for understanding community processes and their resultant biodiversity
 64 patterns (Bell et al. 1995; O'Neil & King 1998; Nakaoka and Noda 2004).

65 One of the effective approaches to understand relative importance of processes
 66 operating at different spatial scales on community structures is to carry out sampling
 67 according to nested, hierarchical design, by setting units of observation at one level of
 68 spatial scale nested within a higher level covering broader spatial scale (Morrissey et al.
 69 1992; Hughes et al. 1999; Noda 2004). This approach is particularly useful for
 70 communities occurring in discrete, patchy manner. For independent single variables
 71 such as abundance and species richness, nested analyses of variance can be used to

detect levels of spatial scale at which the variables in question vary significantly, and to understand relative contribution at different levels to overall variability of the variables (Morrisey et al. 1992; Underwood and Chapman 1996; Hyder et al. 1998; Hughes et al. 1999). For diversity measures, an additive approach using alpha, beta and gamma diversity has been shown to be useful to examine how biodiversity is organized across different spatial scales (Strivastava 1999; Gering and Crist 2002; Karlson et al. 2004; Okuda et al. 2004).

Other important variables for describing variation in community structures include various indices of similarity and dissimilarity that are commonly used for classifying communities (Clarke 1993; Clarke and Warwick 2001). For similarity indices, however, hypothesis-testing approaches using standard statistical procedures such as ANOVA were not applicable for testing variation among samples because data were taken in pairwise manner, violating the assumption of data independence. To overcome this problem, an alternative test was developed based on a non-parametric permutation procedure, termed as ANOSIM test (analysis of similarities; Clarke and Green 1988). ANOSIM can be extended to the hierarchical design covering multiple spatial scales (nested ANOSIM, Clarke 1993). Nested ANOSIM has been increasingly used in recent studies of various types of communities (e.g., Hull 1999; Benedetti-Cecchi et al. 2003a, b; Mumby et al 2004; Van Elven et al 2004).

Among variables for interpreting spatial patterns in community structures, the geographical distance is most simple and useful descriptor to examine how similarity in communities varies spatially (Nekola and White 1999). Generally, similarity in community is expected to decrease with increasing distance because (1) species composition of any communities changes with distance due to limited distributional

ranges of each species reflecting niche-breadth and dispersal ability, and (2) similarity in environmental variables decrease with distance along various environmental gradients (Nekola and White 1999). Distance-similarity relationships have been analyzed recently in some types of communities such as forest and parasitic communities (Nekola and White 1999; Hubbell 2001; Poulin 2003). Most of these analyses, however, were confined to detect patterns at broad spatial scales based on biogeographical data, and little attention has been paid to test whether similar relationships can be found at finer spatial scales, such as within each biogeographical region. A hierarchical sampling design allows to test whether distant-similarity relationship varies with spatial scale of observation.

To understand patterns and processes of scale-dependency in community structures and dynamics, we carried out a quantitative survey of rocky intertidal assemblages encompassing 1800 km along the Pacific coast of Japan (Okuda et al. 2004). The research stations were established according to the hierarchical sampling design that allow comparisons of assemblages at three levels: (1) rock level (the finest spatial scale: encompassing several to hundreds of meters in distance), (2) shore level (the intermediate spatial scale: several to tens of kilometers) and (3) region level (the broadest spatial scale: hundreds to thousands of kilometers). The aims of the present paper are to examine (1) relative contribution of the three spatial scales on variation in similarity of rocky intertidal assemblages, and (2) effect of geographical distance on the observed variation in similarity. We analyzed similarities within and among spatial levels using a cluster analysis and ANOSIM, and tested the relationship between distance and similarity using Mantel test. These analyses were carried out for different groups of organisms (algae, sessile animals and mobile animals) and for different

measures of similarity based on qualitative (presence/absence) data and quantitative data (percent coverage and density) to examine biological and statistical factors affecting the observed patterns.

Materials and methods

Design of census

A hierarchical sampling design (Noda 2004) was employed to compare similarity of rocky intertidal communities at different spatial scales. Six regions were chosen along the Pacific coast of Japan, located between 31°N and 43°N, at intervals of several hundred kilometers (Fig. 1): Osumi (Kagoshima Prefecture; 31°N, 130°E), Nanki (Wakayama Prefecture; 33°N, 135°E), Boso (Chiba Prefecture; 35°N, 140°E), Rikuchu (Iwate Prefecture; 39°N, 142°E), Southern Hokkaido (42°N, 141°E), and Eastern Hokkaido (43°N, 145°E). Within each region, five shores were chosen at intervals of 4 - 25 km alongside the coastline. Within each shore, five permanent stations were established on intertidal rock walls (with angles between 31° and 133° with mean $\pm$ sd of $73.2^\circ \pm 17.7$) that were separated by 5 – 450 m from each other. The total number of stations was thus 150 over the whole research sites. The size of the quadrat at each station was 50 cm horizontal width and 1 m vertical width, with the mean tide located at the middle of the vertical range. Because the angle of rock wall varied, the actual tidal range of the quadrats varied between 20 cm to 50 cm below mean tide for the lowest line, and between 26 cm to 50 cm above mean tide for the highest line. Corners of

Fig.1

each quadrat were marked with plastic or stainless anchors hammered into the rock wall. The position of each station was measured using GPS (Germin, etrex) with an accuracy of 5-10 m deviation.

In July and August 2002, the coverage and presence/absence of all sessile organisms (algae and sessile invertebrates) and the density of mobile animals with limited motility (molluscs and asteroids) were determined during low tide. In each quadrat, percent coverage of sessile organisms were determined by counting the occurrence of sessile organisms at 200 grid points placed at intervals of 5 cm for both vertical and horizontal directions, whereas the numbers of mobile animals were counted by eye. In addition, all species >1 mm within a quadrat were also recorded.

Data analyses

We analyzed presence/absence data and abundance data (coverage of sessile organisms, and density of mobile animals) of all the species that were identified either to species, genus or family. Organisms that were difficult to identify by the visual observation in the field (such as encrusting brown and red algae) were omitted from the analyses, except for coralline algae that were grouped into two operational taxa (articulated calcareous algae and crustose coralline algae).

Similarity of assemblages was calculated for all the pairs of 150 stations (11,175 pairs) for the following six datasets with different combination of data and organism types; (1) presence/absence data of the whole species; (2) presence/absence data of algae; (3) presence/absence data of sessile animals; (4) presence/absence data of

mobile animals; (5) percent coverage data of sessile organisms; and (6) density data of mobile invertebrates. Similarity was calculated using Bray-Curtis index. Prior to this, the percent coverage data were square-root transformed, and the density data were log transformed to reduce excess influence of the dominant species. Cluster analysis was then performed using group-average linkage.

Correlation of similarity data among six datasets were tested using Mantel tests by comparing an observed Pearson correlation coefficient for each pair of similarity matrices against a permutation distribution randomly generated by 10,000 iteration of data. The calculation was carried out using software 'zt' (Bonnet and Van de Peer 2002). To retain an experimentwise error rate at $\alpha = 0.05$, a significant level of each pairwise comparison of the six datasets (a total of 15 comparisons) was determined by setting a comparisonwise error rate at $\alpha' = 0.003$ based on a Bonferroni procedure.

Tests of hierarchical spatial variation in similarity were carried out using two-way nested ANOSIM. ANOSIM tests differences in similarity of community data against null hypothesis that assumes no differences in similarities among factors (Clarke and Warwick 2001). The test static R was defined as:

$$R = \frac{\bar{r}_B - \bar{r}_W}{0.5M}$$

$$M = n(n-1)/2$$

where $\bar{r}_B$ is average of rank similarities from all pairs of replicates *among* different treatments, and $\bar{r}_W$ is average of rank similarities from all pairs of replicates *within* treatments. R is 1 when all replicates within treatments are more similar to each other than any replicates from different treatments, and is approximately 0 when similarities among and within treatments are the same on average. Test of R is conducted by

comparing the R statistic for the observed dataset against to the permutation distribution of data (10,000 iterations in the present study). The ANOSIM can be extended to nested layouts. In the present study, the nested design was employed based on the following two null hypotheses: H_{01} : There are no differences among five shores within each region. H_{02} : There are no differences among six regions. H_{01} was examined by extending the 1-way ANOSIM to a constrained randomization (permutation within each region), and H_{02} by defining the similarity among pairs of regions as the average of all inter-group rank similarities. When significant differences were detected at the regional level, post-hoc comparisons were carried out by pairwise comparisons. The total number of possible permutation between a pair of regions was 126, thus minimum p -value that can be obtained by the analysis was 0.008. Bonferroni procedure requires a comparisonwise error rate of $\alpha' = 0.003$ to retain experimentwise error rate at $\alpha = 0.05$. To minimize excess type I error rate, we defined significant level at $p = 0.008$ for each post-hoc comparison. All the calculations were carried out using the software PRIMER-E (ver. 5; Plymouth Marine Laboratory, UK).

Distance-similarity relationships at each spatial level (among rocks, among shores and among regions) were tested by Mantel test. Direct distances between pairs of stations were calculated based on GPS data. At within-shore level, all pairwise data (10 pairs) were used to construct 5 x 5 matrices at each of 30 shores. At among-shore level, similarity data for 25 pairs of census points for each combination of two shores (5 points/shore x 5 points/shore) were averaged to construct 5 x 5 matrices for each of six regions. Finally at the regional-level, similarity data for 625 pairs of census points for each combination of two regions (25 points/region x 25 points/region) were averaged to construct 6 x 6 matrices. Mantel tests were carried out by comparing an observed

Pearson correlation coefficient against exact permutation distribution (120 combinations for 5 x 5 matrices and 720 for 6 x 6 matrices). The minimum p -value that can be obtained by the analysis was thus 0.008 for the shore-level and the rock-level comparisons. As Mantel test was performed for six regions at the shore-level comparisons and for 30 shores for the rock-level comparisons of each dataset, Bonferroni procedure requires a comparisonwise error rate of $\alpha' = 0.008$ and $\alpha' = 0.002$ for the shore-level and rock-level, respectively, to retain an experimentwise error rate at $\alpha = 0.05$. To minimize excess type I error rate, we defined significant level at $p = 0.008$ for each post-hoc comparison at these two levels.

Variation in distance-similarity relationship among the three organisms groups at the regional level was tested by a randomization test for paired comparison (Manly 1997) using similarity based on the presence-absence data. Similarity of two organism groups at the same geographical distance were paired to obtain Student's t -value for paired data, and the test statistic was compared against a permutation distribution generated by randomly reassigning paired data for 10000 times.

Results

Species composition and abundance

A total of 129 taxa, consisting of 55 algae, 31 sessile invertebrates and 43 mobile invertebrates were identified without taxonomic confusion in the field, and used for the similarity analyses (Table 1). The number of taxa occurred at each region was 32 in

Table 1

Eastern Hokkaido, 42 in Southern Hokkaido, 56 in Rikuchu, 53 in Boso, 52 in Nanki and 50 in Osumi. The number of taxa occurring at each quadrat varied between a maximum of 25 taxa and a minimum of 3 taxa with an average of 14.8 taxa.

Chthamalus barnacles dominated among sessile organisms in Eastern Hokkaido, Southern Hokkaido and Rikuchu, and they were also abundant in Nanki (Fig. 2). Their coverage was 0 % in Boso and Osumi although they were present. A brown algae *Analipus japonicus*, the second dominant species in Eastern Hokkaido, was also abundant in Southern Hokkaido, but it was less abundant in Rikuchu and totally absent from the southern three regions. Articulated calcareous algae was found in all the regions and the most dominant taxon in the three southern regions. A oyster *Saccostrea mordax*, the second dominant species in Osumi was found only in Nanki and Osumi.

For mobile species, a snail *Littorina sitkana* was the most dominant species in Eastern Hokkaido and the second dominant species in Southern Hokkaido (Fig. 2). *Collisella* limpets dominated in Southern Hokkaido and Rikuchu. These two taxa were few or even absent in the southern three regions. In contrast, a limpet *Patelloida saccharina* and a snail *Nerita albicilla*, which were the most dominant species in Boso and Nanki, respectively, did not occurred in the northern three regions.

Cluster analysis

Cluster analyses on similarities among 150 stations revealed clear grouping of community structure by regions (Fig. 3A). Result of a cluster analysis using the

Fig. 2

Fig.3

presence/absence data of all 129 taxa showed that the stations were first grouped into two distinct groups consisting of (1) all the stations in northern three regions (Eastern and Southern Hokkaido and Rikuchu), and (2) those in southern three regions (Boso, Nanki and Osumi). The former was further separated into three groups that corresponded to each of three regions, with a few exceptional stations in Eastern and Southern Hokkaido (Fig. 3C, E). From the southern groups, stations in Boso were clearly separated from those in Nanki and Osumi (Fig. 3A). However, stations in the latter two regions did not separate clearly (Fig. 3D).

Within each regional group, the stations did not group by each shore except for one shore in Boso (B4; Fig. 3B) although the stations from the same shore tended to locate close to each other in most cases (Fig. 3B-E).

Elements of similarity matrices were positively correlated between any pairs of six datasets with different combinations of organism groups (algae, sessile animals and mobile animals) and data types (coverage for sessile organisms and density for mobile animals) (Table 2). Accordingly, results of cluster analyses for these datasets (data not shown) were similar to that for the presence/absence data of all the taxa in points that (1) most of the stations were classified to distinct regional groups except for Nanki and Osumi, and that (2) stations were not distinctly separated by shores within each region.

Table 2

Analyses of similarity

Variation in similarity was significant both among regions and among shores for all the similarity data on different organism groups and on different data types (Table 3). The

Table 3

test statistic R , representing differences in rank similarities between higher and lower hierarchical levels, was nearly twice or much higher for among-region level comparison than among-shore level in all the analyses (Table 3).

Post-hoc comparisons revealed significant differences among pairs of regions except for between the two southern regions (Nanki and Osumi) for all the organism groups and data types. Variation between the two northern regions (Eastern and Southern Hokkaido) was insignificant for the presence/absence data of algae and sessile coverage data (Table 3).

Similarity-distance relationships

A significant negative relationship was found between similarity and distance among pairs of six regions when the similarity was calculated based on the presence/absence data of all the organisms (Table 4). The correlation was also negative for the presence/absence data for sessile and mobile animals and for the density data of mobile animals. The relationship was marginally significant for the presence/absence data of algae and the coverage data of sessile organisms.

Table 4

At among-shore level, the similarity-distance relationship was not significant within each of six regions for any combinations of organism groups and data types except for a significant correlation in one region (Eastern Hokkaido) for the density data of mobile animals (Table 4). Significant negative relationships were also rare in comparisons of among-rock level. Significant negative correlations were detected only at one shore in Southern Hokkaido (S4 in Fig. 1) for the presence/absence data of

the whole species; one shore in Osumi (O5) for the presence/absence data of sessile animals and of mobile animals; and another shore in Southern Hokkaido (S2) for the density data of mobile invertebrates (Table 4). Pearson's correlation coefficient was closer to zero at among-shore and among-rock levels than at among-region level (Table 4).

At the regional level, similarity of mobile animals (based on the presence/absence data) was lower than that of algae and sessile animals particularly at distance over 1000 km (Fig. 4). A randomization test using paired data showed that the similarity of mobile animals were significantly lower than that of algae ($t = 5.807$, $p < 0.001$) and that of sessile animals ($t = 2.410$, $p = 0.032$), whereas the similarity of the latter two organism groups did not differ significantly from each other ($t = 1.692$, $p = 0.115$).

Discussion

The comparisons of rocky intertidal assemblages along the Pacific coast of Japan by the hierarchical sampling design revealed that patterns and magnitude of variation in similarity vary among different spatial scales. The nested ANOSIM found significant variation in similarity both among regions and among shores. The large among-region variation in similarity was depicted by the cluster analysis showing clear grouping of surveyed stations by regions (except for the two southernmost regions). However, the stations were not classified clearly by shores in each region, probably due to smaller degree of variation in similarity at this spatial level compared to that at the lower level

(among rocks). In such cases, interpretation on the degree of variation in similarity based only on descriptive multivariate analyses such as clustering and ordination may lead to equivocal conclusion because they lack model assumptions (Clarke and Green 1988). The hypothesis-testing method using nested ANOSIM based on the hierarchical sampling design is therefore more effective in explicitly evaluating how similarities in assemblages vary with spatial scales.

The results of ANOSIM showed that the degree of variation in similarity was greater among regions than among shores within each region. This suggests that factors operating at broader spatial scale (an extent of several hundreds to thousands of kilometers) are more important in determining assemblage structure than those operating at mesoscale (several to tens of kilometers). The possible contributing factors for the former include oceanic current conditions, climate variation and paleontological processes of marine flora and fauna, whereas the latter includes various local environmental factors such as variation in coastal hydrodynamic regime, wave condition, topography, geology and water quality.

A few preceding studies compared similarity of marine benthic communities by ANOSIM or alternative methods based on hierarchical designs with similar extents and grains of multiple spatial scales to the present study. Underwood and Chapman (1998) investigated rocky intertidal algal assemblages along the 800 km coast of New South Wales, Australia, by setting three levels of observation (between shores separated by hundreds of kilometers, among sites separated by tens of meters, and among quadrats separated by meters), and found greater variability at small spatial scales (among quadrats and between sites) relative to the larger scale differences among shores. Boaventura et al. (2002) compared intertidal rocky shore communities along >800 km

coast of Portuguese by setting four levels of observation (three regions, three shores within a region, three tidal levels within a shore, and five quadrats within each tidal level), and showed great variability in similarity among regions, especially between the northern region and the south and central regions. For subtidal community, Wernberg et al. (2003) compared kelp-associated algal assemblages along >1000 km of southwestern coastline of Australia by setting three levels of comparison (among regions, among sites within regions, and among quadrates within sites), and found that each level of nesting contributed approximately the same to total variation in assemblage structure. Compared to these studies, the results of the present study indicate that broad-scale processes contribute considerably to overall heterogeneity of rocky intertidal assemblages, which may be related to specific oceanic and biogeographical conditions along the coast of Japanese Archipelago. For example, the study sites in New South Wales and Portuguese are exposed to unidirectional ocean currents (Brown and Lomolino 1998), whereas the Pacific coast of Japan is under the influence of more complex current systems.

Oceanic current conditions along the Pacific coast of Japan are affected by two major currents: the warm Kuroshio running along the southwestern coast of the Pacific, and the cold Oyashio running along the eastern coast of Hokkaido to northeastern coast of Honshu, respectively (Kawai 1972; Sugimoto 1990). The cluster analysis showed that the rocky intertidal assemblages were first divided into three northern and three southern groups, which exactly corresponded to the area affected by the two major currents. Paleontological processes may also be responsible for the observed sharp difference between these regions because some taxa evolved in the tropical Indian and

West Pacific regions have possibly intruded only the southern half of Japanese Archipelago (Briggs 1999).

The assemblages were further separated into each regional group except for the two southern regions (Nanki and Osumi). Equivocal separation of the two southern regions by the cluster analysis corresponded to the results of post-hoc tests on ANOSIM showing insignificant differences in similarities between the two regions for all organism groups and data types. These two regions are under the strong influence of the Kuroshio and contain a variety of marine organisms of subtropic origins such as algae *Trichogloea requienii*, a gastropod *Marula musiva* and a bivalve *Saccostrea mordax* (Chihara 1975; Okutani et al. 2000), which possibly lead to similar assemblage structure.

The patterns of regional classifications in our study generally agree to the results of previous studies on biogeography of marine organisms around Japanese waters (Okamura 1928; Chihara 1975; Asakura and Suzuki 1987; Nishimura 1992; Briggs 1995; Asakura 2003). For example, Nishimura (1992) divided coastal areas of Japanese main islands into five biogeographical zones based on information on invertebrate fauna: (1) subarctic, (2) cold temperate, (3) mid temperate, (4) warm temperate and (5) subtropical zones. For algal flora, Chihara (1975) recognized five geographical regions: (1) Eastern Hokkaido, (2) Southern Hokkaido, (3) Northern Pacific coast of Honshu Island, (4) Central Pacific coast of Honshu Island, and (5) Southern Pacific coast of Honshu Island. For both classifications, four northern regions in the present study belong to each of different biogeographical zones, whereas two southern regions locate at the same subtropical zone (or Southern Pacific coast of Honshu Island). The patterns of regional classifications in our study also corresponded

to the results of regional classification of intertidal molluscan assemblage (Asakura and Suzuki 1987). These comparisons demonstrated that broad-scale variation in intertidal assemblage is primarily affected by oceanic and biogeographical variation along the Pacific coast of Japan.

Significant decrease in similarity of communities with geographical distance was discerned at regional level, whereas the relationship was not significant in most of among-shore level and within-shore level comparisons. In general, negative distant-similarity relationship is caused by two major factors, i.e., increasing environmental dissimilarity with distance and biological factors such as limited dispersal ability of organisms (Nekola and White 1999). The non-significant correlations at rock and shore levels suggest either that important environmental factors affecting rocky intertidal assemblages did not vary with distance, or that the dispersal ability or organisms were not important in causing changes in assemblage structure at these spatial scales. For environmental similarities, some important factors for rocky intertidal assemblages, such as wave exposure and water quality, vary with local geographical settings irrespective of distance among different rock walls within each shore and among different rocky shores within each region (M. Nakaoka, T. Noda and T. Yamamoto, personal observations). For the biological factors, the dispersal is less likely to cause the shore-to-shore differences in taxonomic assemblages than the region-to-region difference.

At the regional level, significant negative distance-similarity relationship was discerned in all the organism types and for both qualitative data (presence/absence data) and quantitative data (percent coverage and density data). Notably, the degree of relationships varied among organism groups, with mobile animals showing greater

degree of dissimilarity with distance. The variation in the relationships among different organisms have been shown in other types of communities, such as forest and parasitic community, and ascribed either to different dispersal ability, or to different sensitivities to changes in environmental gradient among organisms (Nekola and White 1999; Poulin 2003). The effect of dispersal ability is unclear because the information of dispersal mode is not available for many taxa in the present study. However, it is likely that mobile and sessile organisms have different sensitivities in response to environmental stress, especially at intertidal habitats subjected to severe physical stresses such as desiccation, thermal stress and wave dispersal. This may be related to different occurrence patterns across geographical ranges, and resultant differences in magnitude of variation in similarity with distance. Species-by-species examination on the distribution and their biology is as a next step to elucidate actual mechanisms causing variation in distance-similarity relationships among different organism groups.

The present study used two different types of data for similarity measure: qualitative presence/absence data and quantitative coverage and density data. Generally, the former varies sensitively with the occurrence patterns of rare species whereas the latter depends more on evenness of dominant species. The similar results between the data types demonstrated the robustness of the analyses of similarities to the different types of data, although it is unknown at the present stage whether the robustness is specific to the present dataset or general to this type of analyses.

In conclusion, the present study revealed patterns and degree of variation in similarities of rocky intertidal assemblages across multiple spatial scales, with the great variation in similarity found at the regional level (hundreds to a thousands kilometer scale) and modest variation at the shore level (several to tens of kilometer scale). The

observed similarity in rocky intertidal assemblages decreased with geographical distance at the regional level, but distance was not a good predictor of changes in assemblages at mesoscale and finest spatial scale. Monitoring on other abiotic and biotic factors by the same hierarchical design will be a next step toward understanding processes and mechanisms causing different patterns of variation in assemblage structures among different spatial scales.

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Table 1 List of taxa identified at 150 stations in six regions along the Pacific coast of Japan

Algae		
CHLOROPHYCEAE	RHODOPHYCEAE (cont.)	BRYOZOA
<i>Collinsiella tuberculata</i>	<i>Champia parvula</i>	<i>Alcyonidium</i> sp.
<i>Enteromorpha intestinalis</i>	<i>Lomentaria hakodatensis</i>	<i>Watersipora subovoidea</i>
<i>Ulva</i> spp.	<i>Centroceras clavulatum</i>	<i>Microporella orientalis</i>
<i>Chaetomorpha moniligera</i>	<i>Ceramium boydenii</i>	
<i>Cladophora</i> spp.	<i>Ceramium</i> sp.	Mobile animals
<i>Urospora penicilliformis</i>	<i>Congregatocarpus pacificus</i>	MOLLUSCA
<i>Boodlea coacta</i>	<i>Chondria crassicaulis</i>	<i>Acanthopleura japonica</i>
<i>Codium fragile</i>	<i>Chondria intertexta</i>	<i>Onithochiton hirasei</i>
	<i>Laurencia</i> spp.	<i>Acanthochitona achates</i>
	<i>Polysiphonia</i> spp.	<i>Cellana toreuma</i>
PHAEOPHYCEAE	Sessile animals	<i>Cellana nigrolineata</i>
<i>Analipus japonicus</i>	PORIFERA	<i>Cellana grata</i>
<i>Dictyota dichotoma</i>	<i>Halichondria japonica</i>	<i>Niveotectura pallida</i>
<i>Ishige okamurae</i>	<i>Halichondria panicea</i>	<i>Patelloida saccharina</i>
<i>Ishige sinicola</i>	<i>Halichondria okadai</i>	<i>Patelloida pygmaea</i>
<i>Leathesia difformis</i>	<i>Haliclona permollis</i>	<i>Lottia cassis</i>
<i>Petrospongium rugosum</i>		<i>Lottia</i> sp.
<i>Melanosiphon intestinalis</i>	CNIDARIA	<i>Collisella</i> spp.
<i>Myelophycus simplex</i>	<i>Dynamena crisioides</i>	<i>Nipponacmea schrenckii</i>
<i>Colpomenia sinuosa</i>	<i>Anthopleura japonica</i>	<i>Nipponacmea fuscoviridis</i>
<i>Alaria crassifolia</i>	<i>Actinia equina</i>	<i>Nipponacmea concinna</i>
<i>Kjellmaniella gyrata</i>		<i>Nipponacmea nigrans</i>
<i>Fucus distichus</i>	ANNELIDA	<i>Nipponacmea habeii</i>
<i>Silvetia babingtonii</i>	<i>Serpulidae</i> spp.	<i>Haliotis diversicolor</i>
<i>Sargassum fusiforme</i>	<i>Dexiospira foraminosa</i>	<i>Montfortula picta</i>
<i>Sargassum thunbergii</i>		<i>Chlorostoma lischkei</i>
RHODOPHYCEAE	MOLLUSCA	<i>Monodonta labio</i>
<i>Nemalion vermiculare</i>	<i>Serpulorbis imbricatus</i>	<i>Monodonta neritoides</i>
articulated calcareous algae	<i>Arcidae</i> spp.	<i>Diloma suavis</i>
crustose coralline algae	<i>Mytilus galloprovincialis</i>	<i>Turbo cornatus</i>
<i>Gelidium divaricatum</i>	<i>Mytilus coruscus</i>	<i>Nerita albicilla</i>
<i>Gelidium elegans</i>	<i>Septifer bilocularis</i>	<i>Planaxis sulcatus</i>
<i>Pterocladia tenuis</i>	<i>Septifer virgatus</i>	<i>Batillaria multiformis</i>
<i>Caulacanthus ustulatus</i>	<i>Hormomya mutabilis</i>	<i>Peasiella habeii</i>
<i>Neodilsea yendoana</i>	<i>Pinctada fucata</i>	<i>Nodilittorina radiata</i>
<i>Gloiopeltis</i> spp.	<i>Crassostrea gigas</i>	<i>Littorina brevicula</i>
<i>Chondracanthus intermedius</i>	<i>Saccostrea kegaki</i>	<i>Littorina sitkana</i>
<i>Chondrus elatus</i>	<i>Saccostrea mordax</i>	<i>Chicoreus brunneus</i>
<i>Chondrus ocellatus</i>	<i>Chama japonica</i>	<i>Cronia margariticola</i>
<i>Chondrus verrucosus</i>		<i>Maculotriton seriale</i>
<i>Chondrus yendoii</i>	ARTHROPODA	<i>Nucella lima</i>
<i>Carpopeltis affinis</i>	<i>Capitulum mitella</i>	<i>Morula granulata</i>
<i>Carpopeltis prolifera</i>	<i>Chthamalus</i> spp.	<i>Morula musiva</i>
<i>Grateloupia imbricata</i>	<i>Tetraclita japonica</i>	<i>Thais bronni</i>
<i>Grateloupia livida</i>	<i>Tetraclita squamosa</i>	<i>Thais clavigera</i>
<i>Polyopes polyideoides</i>	<i>Semibalanus cariosus</i>	<i>Niotha livescens</i>
<i>Prionitis cornea</i>	<i>Balanus albicostatus</i>	<i>Peronia verruculata</i>
<i>Hypnea saidana</i>	<i>Balanus amphitrite</i>	<i>Siphonaria Sirius</i>
<i>Ahnfeltiopsis concinna</i>		<i>Siphonaria japonica</i>

Table 2 Correlations in similarity matrices between pairs of six dataset with different combination of organism groups and data types

	Pearson's correlation coefficient				
	Presence/Absence data				Sessile coverage data
	Total	Algae	Sessile animals	Mobile animals	
Presence/Absence data					
Algae	0.772 ^{***}	-			
Sessile animals	0.556 ^{***}	0.335 ^{***}	-		
Mobile animals	0.869 ^{***}	0.558 ^{***}	0.408 ^{***}	-	
Sessile-organism coverage data	0.688 ^{***}	0.592 ^{***}	0.304 ^{***}	0.612 ^{***}	-
Mobile-animal density data	0.842 ^{***}	0.564 ^{***}	0.429 ^{***}	0.918 ^{***}	0.631 ^{***}

*** Mantel test, $p < 0.001$

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Table 3 Results of nested ANOSIM testing variation in similarity among regions and among shores

	Among regions		Among shores		Post-hoc comparisons among regions [*]
	R	p	R	p	
Presence/Absence data					
Total	0.875	<0.001	0.466	<0.001	E S R B <u>N O</u>
Algae	0.794	<0.001	0.355	<0.001	<u>E S</u> R B <u>N O</u>
Sessile animals	0.713	<0.001	0.181	<0.001	E S R B <u>N O</u>
Mobile animals	0.882	<0.001	0.340	<0.001	E S R B <u>N O</u>
Sessile-organism coverage data	0.811	<0.001	0.360	<0.001	<u>E S</u> R B <u>N O</u>
Mobile-animal density data	0.857	<0.001	0.412	<0.001	E S R B <u>N O</u>

* E: Eastern Hokkaido, S: Southern Hokkaido, R: Rikuchu, B: Boso, N: Nanki, O: Osumi. The pairs of regions without significant differences in similarity connected by underline

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Table 4 Results of Mantel test testing relationships between distance and similarity among each of three spatial levels

Data type	Among regions		Among shores (n=6)		Among rocks (n=30)	
	Pearson's correlation coefficient		Pearson's correlation coefficient (median)	Number of regions with significant negative correlation	Pearson's correlation coefficient (median)	Number of shores with significant negative correlation
	<i>r</i>	<i>p</i>				
Presence/Absence						
Total	-0.702	0.006	0.027	0	-0.266	1
Algae	-0.439	0.074	-0.070	0	-0.245	0
Sessile animals	-0.644	0.006	-0.122	0	-0.197	1
Mobile animals	-0.675	0.010	-0.065	0	-0.061	1
Sessile-organism coverage data	-0.475	0.054	0.011	0	-0.187	0
Mobile-animal density data	-0.662	0.010	-0.393	1	-0.191	1

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Figure Legends

Fig. 1 Study sites established according to the hierarchical sampling design (five shores within each of six regions) along the Pacific coast of Japan. Code for each shore (e.g., E1) given in a way that the first capital letter refers to regions (B: Boso, E: Eastern Hokkaido, N: Nanki, O: Osumi, R: Rikuchu and S: Southern Hokkaido) and the following number to shores within each region (arranged from northeastern to southwestern direction)

Fig. 2 Regional variation in abundance of major taxa (percent coverage for sessile organisms and density for mobile animals) that occurred along the Pacific coast of Japan. Columns and bars denote average and standard deviation of data collected at five shores. B: Boso, E: Eastern Hokkaido, N: Nanki, O: Osumi, R: Rikuchu and S: Southern Hokkaido. 0*: percent coverage was zero but present in the quadrats.

Fig. 3 A dendrogram showing similarities in rocky intertidal assemblages at 150 stations established according to the hierarchical design along the Pacific coast of Japan (A). Enlarged patterns presented for four subgroups (B-E) in which the shores are denoted by the code in Fig. 1

Fig. 4 The relationship between similarity and distance at the regional spatial level. Similarity calculated from the presence/absence data for each group of algae, sessile animals and mobile animals

Fig.1 (Nakaoka et al.)

Fig.2 (Nakaoka et al.)

Fig. 3 (Nakaoka et al.)

Fig.3 (continued) (Nakaoka et al.)

Fig.4 (Nakaoka et al.)