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

7

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23

24

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

45

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

48

**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 (Morrisey 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

72 detect levels of spatial scale at which the variables in question vary significantly, and to  
73 understand relative contribution at different levels to overall variability of the variables  
74 (Morrisey et al. 1992; Underwood and Chapman 1996; Hyder et al. 1998; Hughes et al.  
75 1999). For diversity measures, an additive approach using alpha, beta and gamma  
76 diversity has been shown to be useful to examine how biodiversity is organized across  
77 different spatial scales (Strivastava 1999; Gering and Crist 2002; Karlson et al. 2004;  
78 Okuda et al. 2004).

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

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

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

106         To understand patterns and processes of scale-dependency in community  
107 structures and dynamics, we carried out a quantitative survey of rocky intertidal  
108 assemblages encompassing 1800 km along the Pacific coast of Japan (Okuda et al.  
109 2004). The research stations were established according to the hierarchical sampling  
110 design that allow comparisons of assemblages at three levels: (1) rock level (the finest  
111 spatial scale: encompassing several to hundreds of meters in distance), (2) shore level  
112 (the intermediate spatial scale: several to tens of kilometers) and (3) region level (the  
113 broadest spatial scale: hundreds to thousands of kilometers). The aims of the present  
114 paper are to examine (1) relative contribution of the three spatial scales on variation in  
115 similarity of rocky intertidal assemblages, and (2) effect of geographical distance on the  
116 observed variation in similarity. We analyzed similarities within and among spatial  
117 levels using a cluster analysis and ANOSIM, and tested the relationship between  
118 distance and similarity using Mantel test. These analyses were carried out for different  
119 groups of organisms (algae, sessile animals and mobile animals) and for different

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

123

124

## 125 **Materials and methods**

126

### 127 Design of census

128

129 A hierarchical sampling design (Noda 2004) was employed to compare similarity of  
130 rocky intertidal communities at different spatial scales. Six regions were chosen along  
131 the Pacific coast of Japan, located between 31°N and 43°N, at intervals of several  
132 hundred kilometers (Fig. 1): Osumi (Kagoshima Prefecture; 31°N, 130°E), Nanki  
133 (Wakayama Prefecture; 33°N, 135°E), Boso (Chiba Prefecture; 35°N, 140°E), Rikuchu  
134 (Iwate Prefecture; 39°N, 142°E), Southern Hokkaido (42°N, 141°E), and Eastern  
135 Hokkaido (43°N, 145°E). Within each region, five shores were chosen at intervals of  
136 4 - 25 km alongside the coastline. Within each shore, five permanent stations were  
137 established on intertidal rock walls (with angles between 31° and 133° with mean  $\pm$  sd  
138 of  $73.2^\circ \pm 17.7$ ) that were separated by 5 – 450 m from each other. The total number  
139 of stations was thus 150 over the whole research sites. The size of the quadrat at each  
140 station was 50 cm horizontal width and 1 m vertical width, with the mean tide located at  
141 the middle of the vertical range. Because the angle of rock wall varied, the actual tidal  
142 range of the quadrats varied between 20 cm to 50 cm below mean tide for the lowest  
143 line, and between 26 cm to 50 cm above mean tide for the highest line. Corners of

Fig.1

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

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

154

155

156 Data analyses

157

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

164 Similarity of assemblages was calculated for all the pairs of 150 stations  
165 (11,175 pairs) for the following six datasets with different combination of data and  
166 organism types; (1) presence/absence data of the whole species; (2) presence/absence  
167 data of algae; (3) presence/absence data of sessile animals; (4) presence/absence data of

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

173 Correlation of similarity data among six datasets were tested using Mantel tests  
 174 by comparing an observed Pearson correlation coefficient for each pair of similarity  
 175 matrices against a permutation distribution randomly generated by 10,000 iteration of  
 176 data. The calculation was carried out using software 'zt' (Bonnet and Van de Peer  
 177 2002). To retain an experimentwise error rate at  $\alpha = 0.05$ , a significant level of each  
 178 pairwise comparison of the six datasets (a total of 15 comparisons) was determined by  
 179 setting a comparisonwise error rate at  $\alpha' = 0.003$  based on a Bonferroni procedure.

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

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

184

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

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

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

205 Distance-similarity relationships at each spatial level (among rocks, among  
206 shores and among regions) were tested by Mantel test. Direct distances between pairs  
207 of stations were calculated based on GPS data. At within-shore level, all pairwise data  
208 (10 pairs) were used to construct 5 x 5 matrices at each of 30 shores. At among-shore  
209 level, similarity data for 25 pairs of census points for each combination of two shores (5  
210 points/shore x 5 points/shore) were averaged to construct 5 x 5 matrices for each of six  
211 regions. Finally at the regional-level, similarity data for 625 pairs of census points for  
212 each combination of two regions (25 points/region x 25 points/region) were averaged to  
213 construct 6 x 6 matrices. Mantel tests were carried out by comparing an observed

214 Pearson correlation coefficient against exact permutation distribution (120 combinations  
215 for 5 x 5 matrices and 720 for 6 x 6 matrices). The minimum  $p$ -value that can be  
216 obtained by the analysis was thus 0.008 for the shore-level and the rock-level  
217 comparisons. As Mantel test was performed for six regions at the shore-level  
218 comparisons and for 30 shores for the rock-level comparisons of each dataset,  
219 Bonferroni procedure requires a comparisonwise error rate of  $\alpha' = 0.008$  and  $\alpha' = 0.002$   
220 for the shore-level and rock-level, respectively, to retain an experimentwise error rate at  
221  $\alpha = 0.05$ . To minimize excess type I error rate, we defined significant level at  $p =$   
222 0.008 for each post-hoc comparison at these two levels.

223 Variation in distance-similarity relationship among the three organisms groups  
224 at the regional level was tested by a randomization test for paired comparison (Manly  
225 1997) using similarity based on the presence-absence data. Similarity of two organism  
226 groups at the same geographical distance were paired to obtain Student's  $t$ -value for  
227 paired data, and the test statistic was compared against a permutation distribution  
228 generated by randomly reassigning paired data for 10000 times.

229

230

## 231 **Results**

232

### 233 Species composition and abundance

234

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

Table 1
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238 Eastern Hokkaido, 42 in Southern Hokkaido, 56 in Rikuchu, 53 in Boso, 52 in Nanki  
 239 and 50 in Osumi. The number of taxa occurring at each quadrat varied between a  
 240 maximum of 25 taxa and a minimum of 3 taxa with an average of 14.8 taxa.

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

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

256

257

258 Cluster analysis

259

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

Fig. 2

Fig.3

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

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

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

Table 2
---------

280

281

282 Analyses of similarity

283

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

Table 3
---------

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

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

294

295

296 Similarity-distance relationships

297

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

Table 4
---------

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

310 the whole species; one shore in Osumi (O5) for the presence/absence data of sessile  
311 animals and of mobile animals; and another shore in Southern Hokkaido (S2) for the  
312 density data of mobile invertebrates (Table 4). Pearson's correlation coefficient was  
313 closer to zero at among-shore and among-rock levels than at among-region level (Table  
314 4).

315 At the regional level, similarity of mobile animals (based on the  
316 presence/absence data) was lower than that of algae and sessile animals particularly at  
317 distance over 1000 km (Fig. 4). A randomization test using paired data showed that  
318 the similarity of mobile animals were significantly lower than that of algae ( $t = 5.807$ ,  $p$   
319  $< 0.001$ ) and that of sessile animals ( $t = 2.410$ ,  $p = 0.032$ ), whereas the similarity of the  
320 latter two organism groups did not differ significantly from each other ( $t = 1.692$ ,  $p =$   
321  $0.115$ ).

Fig.4

## 324 Discussion

325  
326 The comparisons of rocky intertidal assemblages along the Pacific coast of Japan by the  
327 hierarchical sampling design revealed that patterns and magnitude of variation in  
328 similarity vary among different spatial scales. The nested ANOSIM found significant  
329 variation in similarity both among regions and among shores. The large among-region  
330 variation in similarity was depicted by the cluster analysis showing clear grouping of  
331 surveyed stations by regions (except for the two southernmost regions). However, the  
332 stations were not classified clearly by shores in each region, probably due to smaller  
333 degree of variation in similarity at this spatial level compared to that at the lower level

334 (among rocks). In such cases, interpretation on the degree of variation in similarity  
335 based only on descriptive multivariate analyses such as clustering and ordination may  
336 lead to equivocal conclusion because they lack model assumptions (Clarke and Green  
337 1988). The hypothesis-testing method using nested ANOSIM based on the  
338 hierarchical sampling design is therefore more effective in explicitly evaluating how  
339 similarities in assemblages vary with spatial scales.

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

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

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

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

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

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

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

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

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

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

429 degree of dissimilarity with distance. The variation in the relationships among  
430 different organisms have been shown in other types of communities, such as forest and  
431 parasitic community, and ascribed either to different dispersal ability, or to different  
432 sensitivities to changes in environmental gradient among organisms (Nekola and White  
433 1999; Poulin 2003). The effect of dispersal ability is unclear because the information  
434 of dispersal mode is not available for many taxa in the present study. However, it is  
435 likely that mobile and sessile organisms have different sensitivities in response to  
436 environmental stress, especially at intertidal habitats subjected to severe physical  
437 stresses such as desiccation, thermal stress and wave dispersal. This may be related to  
438 different occurrence patterns across geographical ranges, and resultant differences in  
439 magnitude of variation in similarity with distance. Species-by-species examination on  
440 the distribution and their biology is as a next step to elucidate actual mechanisms  
441 causing variation in distance-similarity relationships among different organism groups.

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

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

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

459

460

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476

477

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- 591

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

<b>Algae</b>		
<b>CHLOROPHYCEAE</b>	<b>RHODOPHYCEAE (cont.)</b>	<b>BRYOZOA</b>
<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.	<b>Mobile animals</b>
<i>Urospora penicilliformis</i>	<i>Congregatocarpus pacificus</i>	<b>MOLLUSCA</b>
<i>Boodleia 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>
<b>PHAEOPHYCEAE</b>	<i>Polysiphonia</i> spp.	<i>Cellana toreuma</i>
<i>Analipus japonicus</i>	<b>Sessile animals</b>	<i>Cellana nigrolineata</i>
<i>Dictyota dichotoma</i>	<b>PORIFERA</b>	<i>Cellana grata</i>
<i>Ishige okamurae</i>	<i>Halichondria japonica</i>	<i>Niveotectura pallida</i>
<i>Ishige sinicola</i>	<i>Halichondria panicea</i>	<i>Patelloida saccharina</i>
<i>Leathesia difformis</i>	<i>Halichondria okadai</i>	<i>Patelloida pygmaea</i>
<i>Petrospongium rugosum</i>	<i>Haliclona permollis</i>	<i>Lottia cassis</i>
<i>Melanosiphon intestinalis</i>		<i>Lottia</i> sp.
<i>Myelophycus simplex</i>	<b>CNIDARIA</b>	<i>Collisella</i> spp.
<i>Colpomenia sinuosa</i>	<i>Dynamena crisioides</i>	<i>Nipponacmea schrenckii</i>
<i>Alaria crassifolia</i>	<i>Anthopleura japonica</i>	<i>Nipponacmea fuscoviridis</i>
<i>Kjellmaniella gyrata</i>	<i>Actinia equina</i>	<i>Nipponacmea concinna</i>
<i>Fucus distichus</i>		<i>Nipponacmea nigrans</i>
<i>Silvetia babingtonii</i>	<b>ANNELIDA</b>	<i>Nipponacmea habeii</i>
<i>Sargassum fusiforme</i>	<i>Serpulidae</i> spp.	<i>Haliotis diversicolor</i>
<i>Sargassum thunbergii</i>	<i>Dexiospira foraminosa</i>	<i>Montfortula picta</i>
		<i>Chlorostoma lischkei</i>
<b>RHODOPHYCEAE</b>	<b>MOLLUSCA</b>	<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>Maculotriron serriale</i>
<i>Chondrus yendoi</i>	<b>ARTHROPODA</b>	<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,  $p < 0.001$

591

**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</u> O
Algae	0.794	<0.001	0.355	<0.001	<u>E</u> S R B <u>N</u> O
Sessile animals	0.713	<0.001	0.181	<0.001	E S R B <u>N</u> O
Mobile animals	0.882	<0.001	0.340	<0.001	E S R B <u>N</u> O
Sessile-organism coverage data					
Sessile-organism coverage data	0.811	<0.001	0.360	<0.001	<u>E</u> S R B <u>N</u> O
Mobile-animal density data					
Mobile-animal density data	0.857	<0.001	0.412	<0.001	E S R B <u>N</u> O

\* 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

592

**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
	$r$	$p$				
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

593 Figure Legends

594

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

600

601 **Fig. 2** Regional variation in abundance of major taxa (percent coverage for sessile  
602 organisms and density for mobile animals) that occurred along the Pacific coast of Japan.  
603 Columns and bars denote average and standard deviation of data collected at five shores. B:  
604 Boso, E: Eastern Hokkaido, N: Nanki, O: Osumi, R: Rikuchu and S: Southern Hokkaido.  
605 0\*: percent coverage was zero but present in the quadrats.

606

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

611

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

615

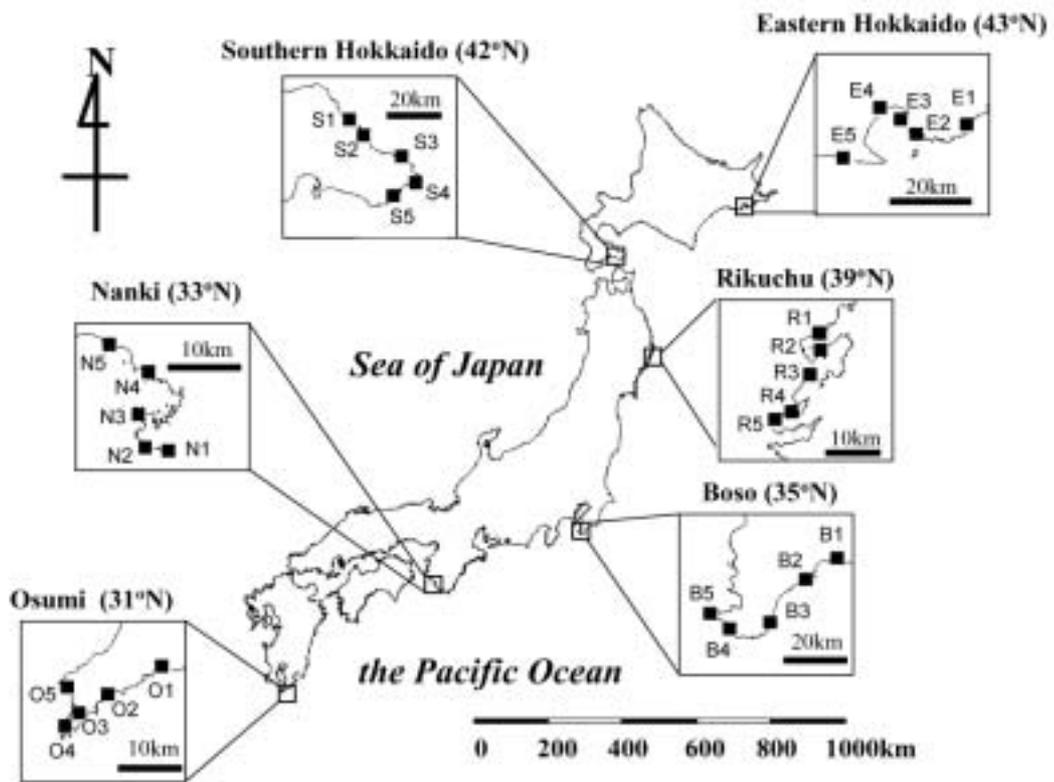
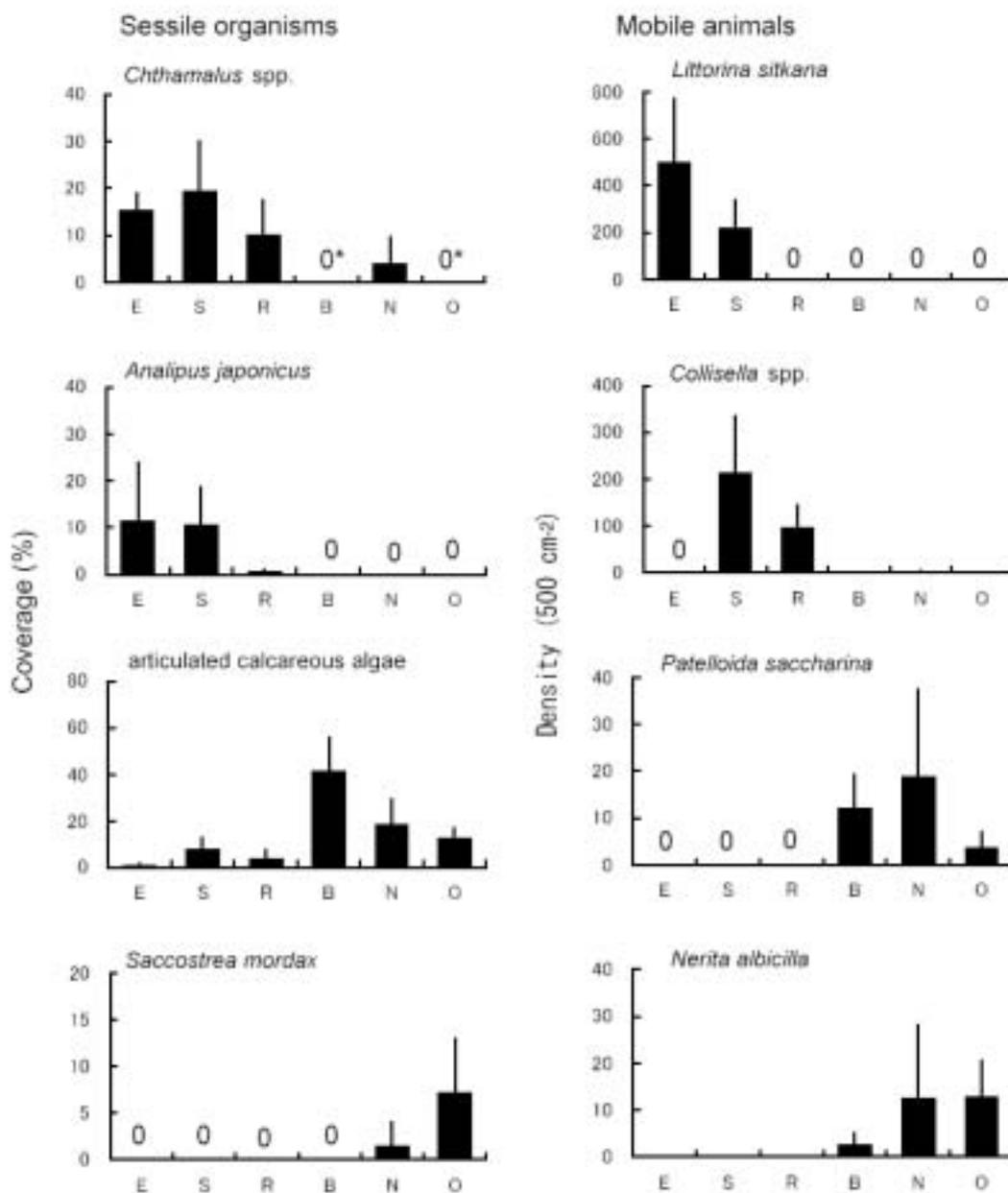


Fig.1 (Nakaoka et al.)

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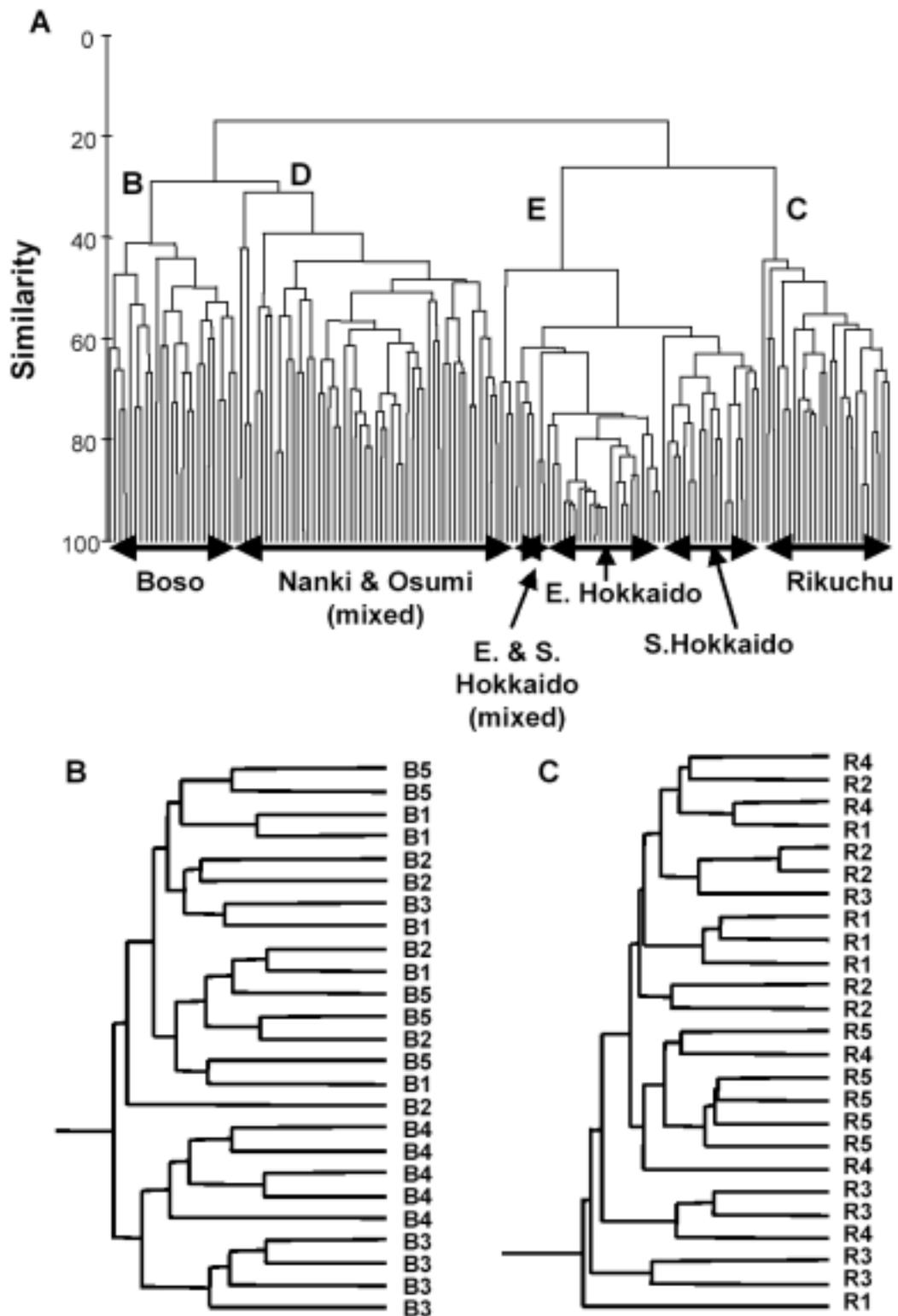
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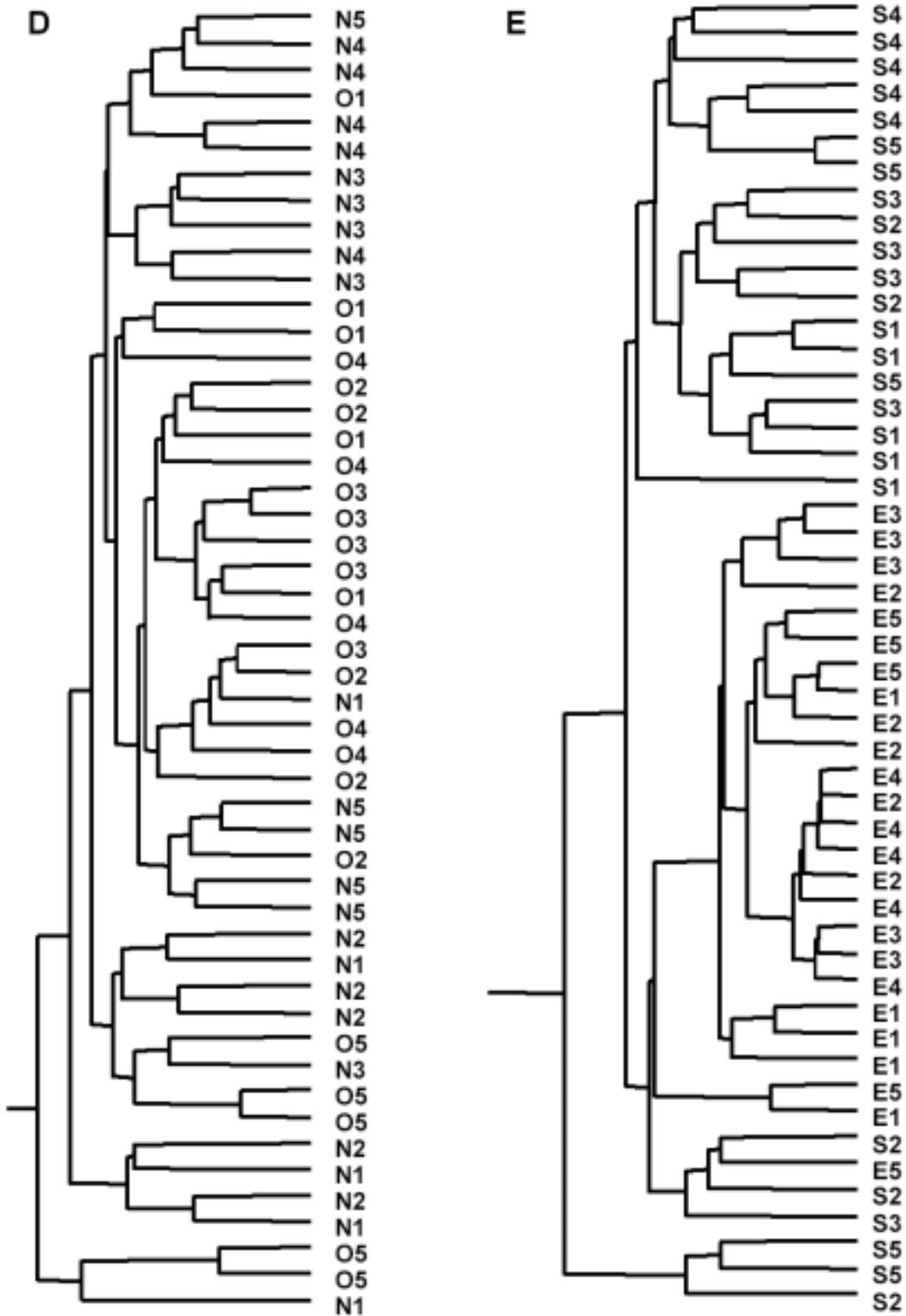
622 Fig.2 (Nakaoka et al.)



623

624

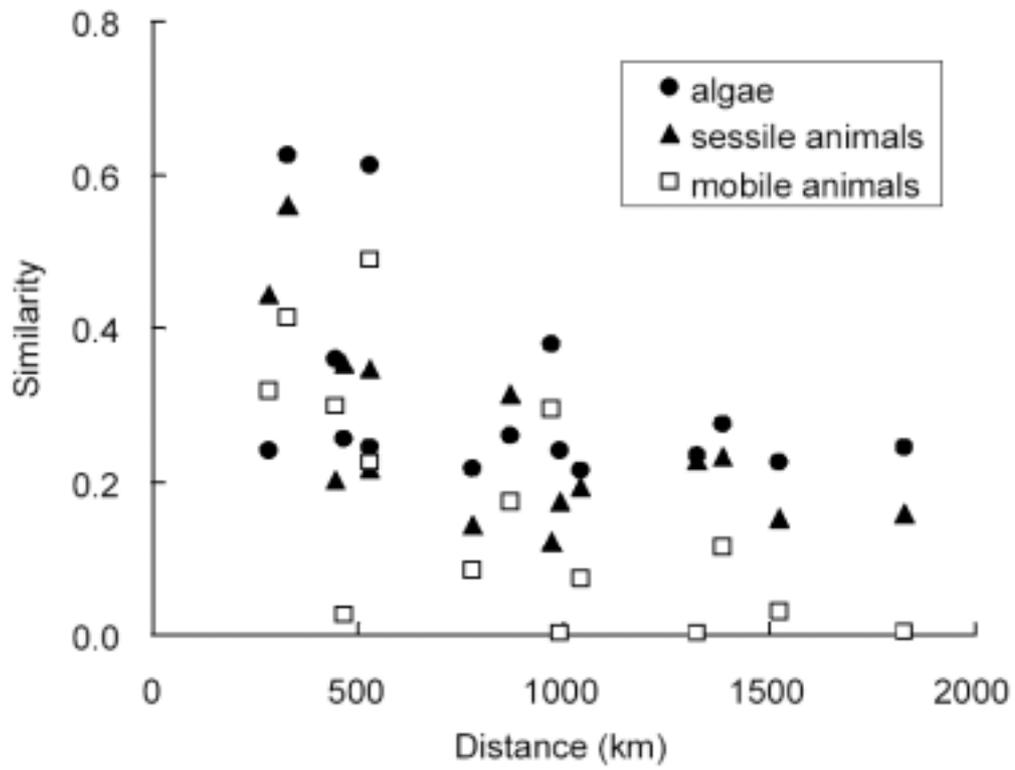
625 Fig. 3 (Nakaoka et al.)



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

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640 Fig.4 (Nakaoka et al.)