

1 *Research Article to MEPS (3rd revision of 201209049, Jan 2013)*

2

3 Multi-scale patterns of spatial variability in sessile assemblage structure do not
4 alter predictably with development time

5

6 Dan A. Smale^{1,2}

7

8 ¹Marine Biological Association of the United Kingdom, The Laboratory, Citadel Hill,
9 Plymouth PL1 2PB, UK

10 ²UWA Oceans Institute & School of Plant Biology, The University of Western Australia,
11 Crawley 6009 WA, Australia

12

13 Correspondence

14 Email: dansma@mba.ac.uk

15 Fax: +44(0)1752633102

16 Phone: +44(0)1752633273

17

18 Running head: spatial variability and assemblage development

19 ABSTRACT

20 Patterns of benthic community structure are driven by a range of biological and physical
21 processes that act over multiple spatial and temporal scales. Spatially nested, hierarchal
22 sampling designs and variance component analyses have been used to examine patterns of
23 multi-scale spatial variability in populations and assemblages and to infer key scale-
24 dependent processes that drive such patterns. Here, settlement panel arrays were deployed in
25 relatively 'pristine' subtidal habitats off southwest Australia, to examine spatial variability in
26 assemblage structure at multiple spatial scales, from centimetres to 100s of kilometres. Panel
27 assemblages were harvested after 3, 9 and 14 months of maturation, to test the following
28 hypotheses: (i) that the magnitude of variability at large spatial scales increases with
29 assemblage development time, (ii) that variability at the smallest spatial scales is consistently
30 high regardless of assemblage development time, and (iii) that patterns of spatio-temporal
31 variability differ between taxa. No clear trends in the magnitude of variability at each spatial
32 scale examined, in relation to assemblage development time, were recorded. Sessile
33 assemblages were highly variable at all spatial scales examined, and variability at the
34 smallest-spatial scale (cms) was consistently high. Although, as predicted, the magnitude of
35 variability at the largest spatial scales (i.e. between locations 100s of km apart) was lowest
36 for immature assemblages, overall patterns of large-scale variability did not alter predictably
37 with assemblage development time and differed between assemblage metrics examined (i.e.
38 multivariate assemblage structure, taxon richness, total cover). Subtidal sessile assemblages
39 in southwest Australia, like elsewhere, are seemingly structured by a complex, interacting
40 suite of biological and physical processes that vary in their relative importance throughout
41 assemblage maturation. As such, predicting spatial variability patterns in ecological structure
42 is challenging, and requires greater appreciation of variability in physical processes across

43 multiple spatial and temporal scales and improved knowledge of the life histories and
44 population structures of key taxa.

45 Key words: Benthic communities, spatial variation, recruitment, temperate reefs, southwest
46 Australia, hierachal designs, variance components

47

48

49 INTRODUCTION

50 Natural communities are structured by a complex suite of interacting physical and biological
51 forces that act across varying spatial and temporal scales (Dayton 1985, Schiel & Foster
52 1986, Levin 1992, Connell 2007). The rate and trajectory of community development, or
53 succession, is strongly influenced by environmental factors (Denslow 1980, Ritter et al.
54 2005), while the relative importance of different processes in structuring communities is
55 influenced by the developmental stage of the community (Sousa 1980). For example, it has
56 long been known that immature communities may respond differently to physical disturbance
57 (Sousa 1980), be more influenced by small-scale abiotic processes that affect recruitment
58 (Underwood & Fairweather 1989) and less influenced by biotic interactions (Connell &
59 Slatyer 1977) than more mature communities. Thus, the relative importance of key abiotic
60 and biotic processes, which act across varying spatial and temporal scales, in structuring a
61 community is mediated to some degree by the maturation stage of that community.

62 In marine ecosystems, ecologists have examined spatial or temporal variability in community
63 structure, at multiple scales, and correlated these patterns with scales of variability in physical
64 and biological factors to make inferences about the relative importance of processes that
65 shape natural communities (Underwood & Chapman 1996, Benedetti-Cecchi et al. 2001).
66 Pronounced variability in community structure at small spatial scales (i.e. centimeters to
67 meters) has emerged as a ubiquitous pattern in coastal ecosystems, whereas the degree of
68 variability over larger spatial scales (i.e. 10s to 100s of kilometers) differs among habitats and
69 taxonomic groups (Fraschetti et al. 2005). Previous studies that have adopted a multi-scale
70 approach have, however, tended to focus on either spatial (e.g. Terlizzi et al. 2007, Smale et
71 al. 2010) or, less commonly, temporal variability (Morrisey et al. 1992), and very few studies
72 have examined the influence of time on multi-scale spatial variability patterns, despite the
73 fact that populations and communities vary concurrently through both time and space (but see

74 Glasby 1998, Hewitt & Thrush 2007). Furthermore, quantitative comparisons of both spatial
75 and temporal variability (e.g. Glasby 1998, Benedetti-Cecchi et al. 2001) have been
76 conducted over relatively short time scales (i.e. weeks to a few months) and have not,
77 therefore, compared assemblages along a broad spectrum of maturity.

78 Immature marine benthic communities are, to a large degree, a product of settlement, post-
79 settlement survival and recruitment processes, which are highly variable at both small
80 (Rodríguez et al. 1993, Edwards & Stachowicz 2011) and large (Gaines & Bertness 1992)
81 spatial scales. As communities mature, biotic interactions become more important so that
82 competitive or facilitative processes may occur over small spatial scales to promote
83 patchiness at the scale of centimeters to meters (e.g. Wahl 2001, Smale et al. 2011c). At
84 larger spatial scales, biotic interactions influenced by variability in the identity and
85 abundance of community dominants or ‘ecosystem engineers’ may promote large-scale
86 variability in ecological pattern (e.g. Fowler-Walker & Connell 2002). Moreover, large-scale
87 ‘between-region’ variability in community structure is likely to increase with community
88 maturity as more ‘unique’ members of the local species pool may colonize the available
89 habitat (Witman et al. 2004).

90 This study aimed to experimentally assess spatial variability patterns at multiple scales, from
91 centimeters to hundreds of kilometers, in the structure of sessile assemblages across
92 developmental stages. To achieve this goal, settlement panels were deployed in subtidal
93 habitats off southwest Australia, which is a global hotspot of marine biodiversity and
94 endemism (Phillips 2001, Tittensor et al. 2010), but relatively poorly understood in terms of
95 early-stage benthic community dynamics (Smale et al. 2011a). The shelf waters off southwest
96 Australia are strongly influenced by the Leeuwin Current (LC), which originates in the Indo-
97 Pacific and flows polewards along the coast of Western Australia, before deviating eastwards
98 into the Great Australian Bight (Pearce 1991, Smith et al. 1991). The LC transports tropical

99 (and subtropical) dispersal stages and warm, nutrient-poor water polewards, which enhances
100 north to south mixing of species and effectively raises winter water temperatures (Ayvazian
101 & Hyndes 1995, Caputi et al. 1996, Smale & Wernberg 2009). Here, sessile assemblages
102 were cultivated in comparatively pristine reef-dominated habitats with minimal human
103 impact (i.e. relative to embayments and harbours) to examine ‘natural’ patterns of spatial
104 variability in relation to assemblage development time.

105 This study tested 3 hypotheses. First, that the magnitude of variability at large spatial scales
106 would increase with assemblage development time. This is because the structure of mature,
107 subtidal reef assemblages is known to vary at scales of 100s of km along the southwest
108 Australian coastline (Wernberg et al. 2003b, Smale et al. 2010). This variability is, at least in
109 part, driven by a well-defined regional-scale temperature gradient (Smale & Wernberg 2009)
110 that influences the local species pool and promotes sequential turnover in assemblage
111 structure along the coastline (Wernberg et al. 2003b, Smale et al. 2010). However, as the
112 coastline is well-connected through oceanography and other key environmental variables
113 (e.g. primary productivity, habitat availability, wave exposure) remain relatively constant
114 across the region (Pearce 1991, Smale & Wernberg 2009), some cosmopolitan species exhibit
115 extensive geographical distributions (e.g. the common kelp *Ecklonia radiata*, see Wernberg
116 et al. 2003a). Thus, it is hypothesized that early-stage assemblages will be characterized by
117 widespread ‘pioneer’ species that are common to local species pools separated by 100s km.
118 As assemblages mature, more species ‘unique’ to the local pool will colonize the artificial
119 habitat, so that the magnitude of large-scale variability increases with time. The second
120 hypothesis is that variability at the smallest spatial scales, centimeters to meters, will be
121 consistently high regardless of assemblage development time, because variability driven by
122 abiotic and biotic forces acting at these scales is a ubiquitous feature of marine benthic
123 assemblages, regardless of assemblage maturity (Fraschetti et al. 2005). The third hypothesis

124 is that patterns of spatio-temporal variability will differ between dominant taxa. Previous
125 research has shown that, even when different species perform similar functions, variability
126 patterns can alter markedly between species because of (sometimes subtle) differences in life
127 histories, which consequently influence successional patterns (e.g. Benedetti-Cecchi 2000,
128 Anderson et al. 2005). In the context of the current study, sessile species of pioneer flora and
129 fauna were predicted to exhibit different spatio-temporal variability patterns because of
130 dissimilarities in life histories, geographical distributions and population structures.

131 **MATERIALS AND METHODS**

132 **Study locations**

133 Colonisation and assemblage development patterns were examined at 2 locations off
134 southwest Australia; Jurien Bay (30°23'40"S, 115° 1'20"E) and Marmion Marine Park
135 (31°45'26"S, 115°41'49"E), which are located 180 km apart (Fig. 1A). At each location, 2
136 comparable study sites were selected 1.0 to 1.5 km apart from one another. All study sites
137 were at 13-15 m depth, 3-5 km offshore and were characterized by a conglomeration of
138 limestone reef and sandy habitats. All sites were moderately exposed to the considerable
139 oceanic swell systems that influence the ecology and geomorphology of the region (Searle &
140 Semeniuk 1985). A series of offshore islands and submerged limestone reefs offer some
141 protected from waves at both locations. The southwest Australian coastline experiences a low
142 magnitude diurnal tidal regime. Subtidal limestone reefs at these locations support a rich flora
143 and fauna that exhibit high levels of diversity and endemism. Reefs surfaces are characterized
144 by stands of large, canopy-forming macroalgae (e.g. the kelp *Ecklonia radiata*), a rich array of
145 understory macroalgae and a high abundance and diversity of reef-associated fish (see
146 Wernberg et al. 2003b, Smale et al. 2010, Langlois et al. 2012 for quantitative descriptions of
147 biodiversity patterns).

148 **Experimental design**

149 Colonisation patterns were examined by deploying standardised artificial substrata (PVC
150 settlement panels) at each site. Although assemblage composition on artificial substrata is
151 known to differ from that on natural substrata (Glasby 2000), a previous study in Marmion
152 Marine Park (Smale et al. 2011c) indicated that assemblages on roughened PVC panels are
153 largely representative of those found on subtidal limestone reefs. Settlement panels were
154 deployed using a moored ring system, modified from Svensson et al. (2007). First, 6 grey
155 settlement panels (200 x 200 mm, 3 mm thick) were attached to an ‘upper’ ring and a ‘lower’
156 ring using cable ties and stainless steel wire. Rings were 800 mm in diameter, constructed
157 from strips of PVC (40 x 2400 mm, 6 mm thick). Panels were attached ~200 mm apart from
158 one another and were suspended >100 mm from the rings. As such, panels within a ring were
159 at least 200 mm apart and at most 800 mm apart. Panels were first roughened with an
160 industrial sandblaster; the duration and areal coverage of sandblasting were standardized. The
161 upper ring was tied to a buoy, while the lower ring was tied to ~20 kg iron weight, which in
162 turn was tethered to a galvanized iron Danforth anchor with 5 m of chain. Thus, each ring
163 comprised 6 independent, inward-facing, vertically orientated settlement panels (Fig. 1B).

164 At each site 7 rings were deployed from a research vessel and then arranged in 3 rows by
165 scuba divers, so that rings were ~7-14 m apart from one another. Rings were deployed on
166 sand to ensure good anchorage and to standardize the immediate habitat. However, rocky
167 habitat (principally low profile platform reef) was observed within 20 m of all panel arrays.
168 Panels were suspended ~2 m from the seabed below the subsurface buoy, at depths of 11 to
169 13 m. Two of the panel rings were randomly selected and retrieved by scuba divers after 3, 9
170 and 14 months of immersion. At ‘Marmion Marine Park site 2’ after both 3 and 14 months, 2
171 panels were lost from one of the rings as a result of damage to the wire and cable ties, so only
172 4 replicates were available for analysis for one of the rings at each of these sampling periods.

173 Panel assemblages on subtidal reefs at these locations are generally complex and well-
174 developed after 14 months (Smale et al. 2011c, Smale 2012), while panel assemblages
175 elsewhere have been shown to reach maturity in considerably less time (e.g. Sugden et al.
176 2008). Panels were checked and maintained regularly (i.e. every ~3 months) during the study
177 period and very few benthic grazers were observed on the panels (i.e. a maximum of 2
178 grazers on all panels within a location). The nested hierarchal design facilitated examination
179 of spatial variability at the scale of 100s of kilometers (between locations), kilometers
180 (between sites), meters (between rings) and centimeters (between panels) as a function of
181 assemblage development time (Fig. 1C).

182 **Analysis**

183 Panels were returned to the laboratory for analysis, where the percent cover of all flora and
184 fauna (>5 mm in size) was estimated using a gridded overlay. A 25 mm perimeter was
185 excluded from analysis to account for ‘edge effects’ (see Todd & Turner 1986 and references
186 therein), providing an analytical area of 150 x 150 mm for each panel. Macro images of flora
187 and fauna were collected, and voucher specimens of all discernible taxa were taken and
188 preserved accordingly to aid identification. All sessile organisms were identified to the lowest
189 taxonomic level possible (generally species for macroalgae and family or genus for fauna). In
190 this manner, 41 distinct faunal groups (comprising principally of ascidians and bryozoans)
191 and 19 floral groups (principally red algae) were used to quantify assemblage structure on the
192 panels.

193 Patterns of spatial variability in assemblage structure over time were initially examined with
194 a four-factor design using permutational multivariate analysis of variance (PERMANOVA,
195 see Anderson 2001). Factors were: ‘Month’ (fixed, crossed with ‘Location’), ‘Location’
196 (random), ‘Site’ (random, nested within ‘Location’) and ‘Ring’ (random, nested within

197 ‘Site’). Permutations were based on a Bray-Curtis similarity matrix generated from square-
198 root transformed percent cover data; the transformation was used to down-weight the
199 influence of large space occupiers. Tests used up to 4999 permutations under a reduced
200 model and significance was accepted at $P < 0.05$. A PCO plot based on the Bray-Curtis
201 similarity matrix was used to visualize shifts in multivariate structure through time and space.
202 To investigate the influence of development time on spatial variability further, differences
203 between spatial scales were examined for each sampling period (i.e. 3, 9 and 14 months)
204 using a fully nested hierarchal design (i.e. ‘Location’, ‘Site’ and ‘Ring’, all random and
205 spatially nested). As fully nested sampling designs provide biased and independent
206 assessments of variability across multiple spatial scales (Underwood & Chapman 1996) this
207 approach allowed (pseudo) variance components to be compared between spatial scales and
208 across sampling periods. Where negative various components were generated, they were re-
209 set to zero (Benedetti-Cecchi 2001). Variability in univariate metrics, including total cover,
210 taxon richness and the cover of dominant taxa, was also tested with PERMANOVA, using
211 the model described above (but with matrices based on Euclidean distances of untransformed
212 data, which is analogous to traditional ANOVA). As many statistical tests were conducted,
213 the probability of falsely rejecting at least one null hypothesis would have been greater than
214 the conventional alpha value of 0.05. Rather than employ sequential Bonferroni corrections,
215 which may be overcautious and impractical for this type of study (Moran 2003), variability
216 was deemed significant at $P \leq 0.01$ to reduce the risk of Type 1 error. Even so, conducting >20
217 sequential tests increases the chance of Type 1 error and, as such, the tests were used to
218 examine general variability patterns across sampling times and taxa, rather than generating
219 specific significance values. Finally, for each location differences in multivariate dispersion
220 within sampling periods was tested with PERMDISP, which essentially tests for homogeneity
221 of variance across levels of a given factor (in this case ‘Month’). All analysis was conducted

222 with PRIMER 6 (Clarke & Warwick 2001), using the PERMANOVA add-on (Anderson et
223 al. 2008).

224 **RESULTS**

225 Sessile assemblage structure changed with development time, as assemblages after 3 months
226 were distinct from those after 14 months at both locations (Fig. 2). This was particularly
227 evident at Marmion Marine Park, where assemblage structure shifted sequentially through
228 time (Fig. 2). The full PERMANOVA model detected a highly significant interaction
229 between development time ('Month') and 'Site' (Table 1), and examination of the PCO plot
230 showed that patterns of temporal change in assemblage structure at Jurien Bay varied
231 considerably between sites (Fig. 2). The PCO plot also suggested that the direction of
232 assemblage development differed between the study locations. In general, sessile
233 assemblages at Marmion Marine Park comprised more macroalgae than at Jurien Bay, and
234 tended to shift from a low-richness pioneer assemblage towards a high coverage, moderate
235 richness, macroalgal dominated assemblage (Fig. 3). Conversely, assemblages at Jurien Bay
236 were more fauna-dominated, with variable but occasionally high areal coverage of sponges,
237 bivalves and bryozoans (Fig. 3). With regards to heterogeneity in assemblage structure over
238 time, within-group multivariate dispersion was significantly different between months at both
239 Marmion Marine Park and Jurien Bay (Table 2). Within both locations, assemblages were
240 least heterogeneous after 3 months and most heterogeneous after 9 and 14 months (Table 2).

241 Patterns of multi-scale spatial variability were subsequently examined separately for each
242 month with PERMANOVA. For multivariate assemblage structure, between-location (i.e.
243 100s km) variability was non-significant for all months, whereas significant between-ring
244 variability (i.e. meters) was recorded for all months. Significant variability at the intermediate
245 scale of site (i.e. ~1 km) was also recorded at 3 and 9 months (Table 3). Examination of the

246 pseudo-variance components generated from the PERMANOVA model indicated no clear
247 pattern in the contribution of variance components to total variability over time, although
248 large-scale variability was markedly low for immature 3 month old assemblages (Fig. 4A).
249 Variability at the smallest spatial scale, (i.e. between panels, ~20 cm apart) was consistently a
250 principal source of spatial variability (Fig. 4A).

251 Patterns of spatial variability for assemblage-level univariate metrics (i.e. total cover and
252 taxon richness) were similarly inconsistent through time (Table 3, Fig. 4B&C). Total cover
253 varied significantly only at the smallest scale of ring after 3 months and the largest scale of
254 location after 9 months (Table 3). This was also reflected in the pseudo-variance components,
255 as variability at the smallest scales of ring and panel were major contributors to total
256 variability, whilst variability between locations was only prominent for the 9 month samples
257 (Fig. 4B). Plots of mean total cover for each site showed that total cover was considerably
258 greater at Marmion Marine Park after 9 months, but not after 3 or 14 months (Fig. 5A).

259 Taxon richness varied significantly only at the scale of site after 3 months and at the scale of
260 location after 9 months (Table 3). This was clearly reflected in the pseudo-variance
261 components, as variability at the scale of site was pronounced after 3 months and variability
262 between locations was prominent after 9 months (Fig. 4C). As with total cover, variability at
263 the scale of panel was consistently a major contributor to total observed variability in taxon
264 richness (Fig. 4C). Plots of mean taxon richness for each site showed that richness varied
265 considerably between the sites at Jurien Bay after 3 months, and thereafter richness was
266 markedly greater at Marmion Marine Park compared with Jurien Bay (Fig. 5B).

267 Spatial variability patterns were also examined for the 4 most abundant taxa (Table 3, Fig.
268 5C-F). The bryozoan *Triphyllozoon moniliferum* demonstrated a general increase in percent
269 cover over time (Fig. 5C) and was a major space occupier after 14 months, covering almost
270 20% of available space at Jurien Bay. The cover of *T. moniliferum*, however, varied markedly

271 between sites, so that after 14 months its spatial coverage differed by a factor of ~20 between
272 the two sites at Jurien Bay (Fig. 5C). Indeed, significant variability in the cover of *T.*
273 *moniliferum* between sites was recorded after 3 months and 14 months, but not after 9 months
274 (Table 3). The serpulid polychaete, *Hydroides* sp. a, was sampled at every site and sampling
275 period, being a ubiquitous component of the sessile assemblages (Fig. 5D). Significant
276 variability in the cover of *Hydroides* sp. a was observed between sites and rings after 3
277 months, and rings after 14 months (Table 3). The bivalve *Ostrea angasi*, which was common
278 at Jurien Bay, varied significantly at the scale of ring after 3 and 9 months and at the scale of
279 site after 14 months (Fig. 5E, Table 3). Finally, the bivalve *Anomia trigonopsis*, which was
280 common at both locations, varied significantly among sites after 3 months (Fig. 5F, Table 3).
281 In general, taxon-specific spatial variability patterns were largely inconsistent between taxa
282 and showed no clear trend through time. However, significant variability was recorded more
283 often after 3 months, compared with 9 and 14 months, and significant variability at
284 intermediate to small spatial scales (i.e. site and ring) was recorded more often than at the
285 largest scale of location (Table 3).

286 **DISCUSSION**

287 The first hypothesis, that the magnitude of large scale variability would increase with
288 assemblage development time, was partially supported in that between-location variability in
289 multivariate assemblage structure and taxon richness was considerably lower after 3 months
290 compared with 9 and 14 months. In southwest Australia, variability in the structure and
291 richness of mature macroalgal assemblages on subtidal reefs at this spatial scale has been
292 documented previously (Wernberg et al. 2003b, Smale et al. 2010, Smale et al. 2011b). The
293 Leeuwin Current generates a regional-scale temperature gradient and enhances the north-
294 south mixing of species, so that benthic assemblage composition shifts fairly predictably
295 along the coastline (Smale et al. 2010, Langlois et al. 2012). Moreover, variability in the

296 Leeuwin Current and its eddies influences particle retention rates, so that some coastal areas
297 retain larvae and propagules more than others. A particle tracking study by Feng et al. (2010)
298 indicated that dispersive bodies are retained within the Perth coastal region (which
299 encompasses Marmion Marine Park) to a greater extent than within the Jurien Bay region,
300 which would influence the number and identity of larvae and propagules available for
301 settlement. As such, the 2 study locations would, to some extent, support distinct local
302 species pools that are available to colonize new habitat, which would promote between-
303 location variability. In addition, the fact that assemblages at Jurien Bay were more fauna-
304 dominated and less flora-dominated than those at Marmion Marine Park could indicate
305 differences in light-attenuation or nutrient/food availability between locations. Although there
306 are no reported differences in primary productivity, nutrient levels or light availability
307 between these locations (Wernberg et al. 2005, Koslow et al. 2008, Wernberg unpublished
308 data), it is plausible that local-scale variation in, for example, turbidity, influences the
309 development of sessile assemblages.

310 The magnitude of large-scale variability did not, however, increase predictably with
311 development time but instead peaked after 9 months when between-location variability in
312 assemblage structure, total cover and taxon richness was the major contributor to total
313 variability. As 9 month panel assemblages were harvested towards the end of the austral
314 winter, whereas 3 and 14 month assemblages were harvested in late summer, localised
315 seasonal influences may have promoted between-location variability. For example, at
316 Marmion Marine Park total cover and taxon richness peaked after 9 months, being
317 significantly greater than at Jurien Bay. While Marmion Marine Park is relatively unimpacted
318 by human activities and nutrient levels are low compared with many other temperate coastal
319 systems (Lourey et al. 2006), the Perth Metropolitan Area (1.7 million inhabitants) sprawls
320 northwards along the bounding coastline so that anthropogenic influences are likely to be

321 substantially greater than at Jurien Bay (1500 inhabitants). It could be that increased nutrient
322 levels through the winter rainy season, as a result of terrestrial run-off (Lourey et al. 2006),
323 sediment resuspension during storms (Lourey et al. 2006), groundwater discharge (Johannes
324 & Hearnnes 1985) or effluent outlets (Thompson & Waite 2003), promoted macroalgal growth
325 on panels in Marmion but not in Jurien, thereby creating seasonality in the magnitude of
326 variability between locations. Repeating these experiments with initial panel deployments in
327 different seasons would elucidate the degree of seasonality in patterns of multi-scale spatial
328 variability with assemblage development time.

329 The second hypothesis, that the magnitude of small-scale variability would be consistently
330 high regardless of assemblage maturity, was supported. Variability at the spatial scale of
331 centimetres (i.e. between panels within rings) was consistently a major contributor to total
332 observed variability for all the assemblage-level metrics examined. Pronounced variability in
333 populations and assemblages at this spatial scale has been documented many times before,
334 primarily in intertidal or very shallow subtidal habitats, suggesting that local biological
335 interactions and small-scale physical processes are characteristic of marine systems
336 (Underwood & Chapman 1996, Benedetti-Cecchi 2001, Coleman 2002, Fraschetti et al.
337 2005). In intertidal habitats, variability at the scale of centimetres may be promoted by habitat
338 heterogeneity, which in turn influences sedimentation, desiccation stress, wave action and
339 predation pressure (Coleman 2002, Fraschetti et al. 2005). Moreover, recruitment of habitat-
340 forming species may vary across similar spatial scales in shallow subtidal habitats (e.g.
341 Kendrick & Walker 1995), promoting variability in both populations and assemblages (but
342 see Coleman 2003).

343 In the current study, habitat structure and orientation was standardised with the use of
344 suspended settlement plates, suggesting that processes other than habitat structure varied
345 across small spatial scales. Variability in settlement and recruitment can occur at very small

346 to very large spatial scales, as it is influenced by physical processes ranging from micro-scale
347 boundary layer flow (Mullineaux & Butman 1990) through to regional-scale ocean current
348 dynamics (Gaines & Bertness 1992). As small-scale variability was consistently high for 3, 9
349 and 14 month assemblages, it cannot be attributed to recruitment variability alone, although
350 small-scale patterns of water movement around panels and rings would almost certainly have
351 been important. As such, biological interactions, including ‘priority effects’ (i.e. where the
352 identity of early colonists influences subsequent patterns of assemblage development, see
353 Benedetti-Cecchi 2000 and references therein) may have promoted variability between
354 panels. Certainly, stochastic recruitment of the dominant kelp in the region, *Ecklonia radiata*,
355 influences the structure of developing assemblages (Smale et al. 2011c). Biotic interactions,
356 both positive and negative, would certainly have influenced assemblage structure at Marmion
357 Marine Park after 9 months, where >15 sessile taxa occupied >60% of panel surfaces. Large,
358 structural organisms (e.g. macroalgae, demosponges, ascidians) can influence the structure of
359 surrounding benthic assemblages, by altering fine-scale water movement and light levels
360 (Kendrick et al. 1999, Wernberg et al. 2005, Toohey et al. 2007), and it is plausible that
361 colonisation by some taxa would have promoted between-panel variability in assemblage
362 development trajectories.

363 Variability in grazing and predation pressure has long been known to promote variability in
364 benthic assemblage structure at multiple spatial scales (e.g. Paine & Vadas 1969, Andrew
365 1993). In southwest Australia, however, invertebrate herbivores are generally low in
366 abundance and exhibit highly patchy distributions (Vanderklift & Kendrick 2004, Wernberg
367 et al. 2008), so that direct grazing pressure is thought to be relatively weak (Smale et al.
368 2011a). Moreover, as the panels were suspended above the seabed and very few invertebrate
369 grazers or predators (e.g. molluscs, echinoderms) were observed on the panels, it seems
370 unlikely that variability in consumer pressure promoted small to medium scale variability.

371 The design of the moored ring structure would have restricted access to panel assemblages
372 for large demersal fish (e.g. the Silver Drummer, *Kyphosus sydneyanus*), but smaller
373 demersal fish may have preferentially consumed sessile organisms on certain panels or rings
374 and influenced variability patterns. However, there was little evidence of direct feeding on
375 panels at these study locations, and top down processes are assumed to be weak at most
376 locations along the temperate coastline of Western Australia (but see Smale 2012).
377 Ultimately, focussed experimental manipulation is required to test the underlying mechanistic
378 processes driving both small and large scale variability (Underwood 1990).

379 For multivariate assemblage structure, site-level variability was a major contributor to total
380 variability after 3 and 14 months, but not 9 months, and taxon richness varied significantly
381 between sites only after 3 months. Pronounced variability in sessile assemblage development
382 at the scale of kilometres has been observed previously in relatively pristine subtidal systems
383 (Glasby 1998, Bowden et al. 2006). It is likely that the between-site variability observed at
384 Jurien Bay after 3 months was, at least partly, caused by recruitment variability or proximity
385 to source populations, so that assemblages at one of the study sites were structurally distinct
386 and more diverse. As the sites selected were similar in terms of habitat type, proximity to reef
387 and surrounding benthic assemblages, variability in local water movement and the supply of
388 recruits remains the most plausible explanation for ecological variability at the scale of ~1
389 km. Interestingly, structural differences were again evident after 14 months, suggesting that
390 post-recruitment processes such as competition, light or food availability varied among sites.

391 The final hypothesis was supported as spatial variability patterns differed between dominant
392 species, presumably due to different life history characteristics, from timing of reproduction
393 through to growth and competitive ability (Butler 1986, Glasby 1998, Benedetti-Cecchi et al.
394 2001). After 3 months, however, all species varied significantly between sites, again
395 suggesting the importance of recruitment variability at the scale of kilometres (e.g. Glasby

1998, O’Leary & Potts 2011). Pronounced between-site variability persisted through maturation for all species, perhaps as a consequence of initial recruitment variability. The assemblage dominants examined were all pioneer species, having long-lived planktotrophic larvae with high dispersal potential (as inferred from congeners, see below), and are fairly typical components of sessile assemblages in southwest Australia (Chalmer 1982, Smale 2012). Although species-specific information on the timing of reproduction, larval duration and dispersal potential is lacking, information on closely related species can be used to cautiously infer important life history traits. For example, *Anomia ephippium* exhibits pulsing recruitment throughout the year (Bramanti et al. 2003), whereas larval release and recruitment of *Ostrea* species is generally highly seasonal (Wilson & Simons 1985, Fournier 1992). This seems to be reflected in the occurrence of congeners off southwest Australia, as *Anomia trigonopsis* was present at low cover in all sampling periods, whereas the cover *Ostrea angasi* was considerably more variable in time. As such, differences in species cover with time were perhaps due to timing and modes of larval release (i.e. continuous, pulsing or highly seasonal), while relatively low variability between locations was mostly likely attributable to the high reproductive and dispersal capabilities of these pioneer species. Similarly, serpulid worms – including the genus *Hydroides* – are typical early-colonisers, exhibiting high reproductive output, dispersal potential and growth rates, as well as broad environmental tolerances (Grave 1933, Qui & Qian 1997). In the current study, the recruitment of *Hydroides* spp. onto panels was spatially variable but considerably greater during the early stages of community development, as would be expected of this pioneer genus. In contrast, the bryozoan *Triphyllozoon moniliferum*, which appears to function as a mid-successional species in sessile assemblages in temperate Australia (Butler & Connolly 1996) and presumably exhibits distinct life history traits (see Bock 1982 for an account of the

420 Australian Phidoloporidae), was again spatially variable but much more abundant at the latter
421 stages of community development encompassed by the study.

422 In conclusion, the structure of sessile assemblages varied at multiple spatial scales and
423 patterns of variability were neither consistent with, nor predictably affected by, assemblage
424 development time. The hypothesis that large scale variability would increase with community
425 development time was not fully supported, whereas the hypothesis that small scale variability
426 would be ubiquitous was supported. It was also evident that spatio-temporal variability
427 patterns vary between taxa. In marine ecosystems, assemblages are influenced by a complex
428 suite of interacting physical and biological processes that act over varying spatial and
429 temporal scales. In southwest Australia, key processes that influence subtidal sessile
430 assemblages act at spatial scales ranging from regional climate variability, driven by
431 fluctuations of the Leeuwin Current (Kendrick et al. 2009, Wernberg et al. 2012), through to
432 small-scale biotic interactions mediated by habitat heterogeneity at the scale of meters or less
433 (Wernberg et al. 2005, Toohey et al. 2007). Clearly, hierarchical analyses of spatial variability
434 can provide insights into processes that may influence organisms and assemblages and help
435 to focus experimental work on key processes at relevant scales (Benedetti-Cecchi 2001). In
436 the coastal ecosystem off southwest Australia, as elsewhere, assemblages are highly variable
437 at multiple spatial scales and the relative importance of structuring processes may vary
438 unpredictably with time. This study further emphasises the need for ecologists to adopt a
439 multi-scale approach when describing patterns of benthic community structure and
440 elucidating the processes that drive them.

441 *Acknowledgements:* I thank Gary Kendrick, Renae Hovey and Anne Brearley for their
442 taxonomic expertise and Thibault De Bettignes, Alex Grochowski, Samantha Childs, Renae
443 Hovey, John Statton, Kris Waddington, Ben Saunders, Laura Fullwood, Bryce McLaren,
444 Adam Gartner, Scott Bennett, Jordan Goetze and Anthony Payne for assistance in the field.

445 This research was supported by a Research Development Award from the University of
446 Western Australia and a Marie Curie International Incoming Fellowship within the 7th
447 European Community Framework Programme.

448

449 LITERATURE CITED

- 450 Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance.
451 *Austral Ecol* 26:32-46
- 452 Anderson MJ, Diebel CE, Blom WM, Landers TJ (2005) Consistency and variation in kelp
453 holdfast assemblages: Spatial patterns of biodiversity for the major phyla at different
454 taxonomic resolutions. *J Exp Mar Biol Ecol* 320:35-56
- 455 Anderson MJ, Gorley RN, Clarke KR (2008) *PERMANOVA+ for primer: guide to software and*
456 *statistical methods*. PRIMER-E, Plymouth, UK
- 457 Andrew NL (1993) Spatial heterogeneity, sea urchin grazing, and habitat structure on reefs in
458 temperate Australia. *Ecology* 74:292-302
- 459 Ayvazian SG, Hyndes GA (1995) Surf-zone fish assemblages in south-western Australia: do
460 adjacent nearshore habitats and the warm Leeuwin Current influence the
461 characteristics of the fish fauna? *Mar Biol* 122:527-536
- 462 Benedetti-Cecchi L (2000) Priority effects, taxonomic resolution, and the prediction of
463 variable patterns of colonisation of algae in littoral rock pools. *Oecologia* 123:265-
464 274
- 465 Benedetti-Cecchi L (2001) Variability in abundance of algae and invertebrates at different
466 spatial scales on rocky sea shores. *Mar Ecol Prog Ser* 215:79-92
- 467 Benedetti-Cecchi L, Rindi F, Bertocci I, Bulleri F, Cinelli F (2001) Spatial variation in
468 development of epibenthic assemblages in a coastal lagoon. *Est Coast Shelf Sci*
469 52:659-668
- 470 Bock PE (1982) Bryozoans. In: Shepherd SA, Thomas IM (eds) *Marine invertebrates of*
471 *southern Australia Part 2*. D.J. Woolman, Govt. Printer
- 472 Bowden DA, Clarke A, Peck LS, Barnes DKA (2006) Antarctic sessile marine benthos:
473 colonisation and growth on artificial substrata over three years. *Mar Ecol Prog Ser*
474 316:1-16
- 475 Bramanti L, Magagnini G, Santangelo G (2003) Settlement and recruitment: The first stages
476 in the life cycle of two epibenthic suspension feeders (*Corallium rubrum* and *Anomia*
477 *ephippium*). *Ital J Zoo* 70:175-178
- 478 Butler AJ (1986) Recruitment of sessile invertebrates at five sites in Gulf St. Vincent, South
479 Australia. *J Exp Mar Biol Ecol* 97:13-36
- 480 Butler AJ, Connolly RM (1996) Development and long term dynamics of a fouling
481 assemblage of sessile marine invertebrates. *Biofouling* 9:187-209
- 482 Caputi N, Fletcher WJ, Pearce A, Chubb CF (1996) Effect of the Leeuwin Current on the
483 recruitment of fish and invertebrates along the Western Australian coast. *Mar*
484 *Freshwater Res* 47:147-155
- 485 Chalmer PN (1982) Settlement patterns of species in a marine fouling community and some
486 mechanisms of succession. *J Exp Mar Biol Ecol* 58:73-85
- 487 Clarke KR, Warwick RM (2001) *Change in marine communities: an approach to statistical*
488 *analysis and interpretation*. PRIMER-E, Plymouth, UK

489 Coleman MA (2002) Small-scale spatial variability in intertidal and subtidal turfing algal
490 assemblages and the temporal generality of these patterns. *J Exp Mar Biol Ecol*
491 627:53-74

492 Coleman MA (2003) The role of recruitment in structuring patterns of small-scale spatial
493 variability in intertidal and subtidal turfs. *J Exp Mar Biol Ecol* 291:131-145

494 Connell JH, Slatyer RO (1977) Mechanisms of succession in natural communities and their
495 role in community stability and organization. *Am Nat* 111:1119-1144

496 Connell SD (2007) Subtidal temperate rocky habitats: habitat heterogeneity at local to
497 continental scales. In: Connell SD, Gillanders BM (eds) *Marine Ecology*. Oxford
498 University Press, Melbourne

499 Dayton PK (1985) Ecology of kelp communities. *Ann Rev Ecol Syst* 16:215-245

500 Denslow JS (1980) Patterns of plant species diversity during succession under different
501 disturbance regimes. *Oecologia* 46:18-21

502 Edwards KF, Stachowicz JJ (2011) Spatially stochastic settlement and the coexistence of
503 benthic marine animals. *Ecology* 92:1094-1103

504 Feng M, Slawinski D, Beckley LE, Keesing JK (2010) Retention and dispersal of shelf
505 waters influenced by interactions of ocean boundary current and coastal geography.
506 *Mar Freshwater Res* 61:1259-1267

507 Fournier M-L (1992) The reproductive biology of the tropical rocky oyster *Ostrea iridescens*
508 (Bivalvia: Ostreidae) on the Pacific coast of Costa Rica. *Aquaculture* 101:371-378

509 Fowler-Walker MJ, Connell SD (2002) Opposing states of subtidal habitat across temperate
510 Australia: consistency and predictability in kelp canopy-benthic associations. *Mar*
511 *Ecol Prog Ser* 240:49-56

512 Fraschetti S, Terlizzi A, Benedetti-Cecchi L (2005) Patterns of distribution of marine
513 assemblages from rocky shores: evidence of relevant scales of variation. *Mar Ecol*
514 *Prog Ser* 296:13-29

515 Gaines SD, Bertness MD (1992) Dispersal of juveniles and variable recruitment in sessile
516 marine species. *Nature* 360:579-580

517 Glasby TM (1998) Estimating spatial variability in developing assemblages of epibiota on
518 subtidal hard substrata. *Mar Freshwater Res* 49:429-437

519 Glasby TM (2000) Surface composition and orientation interact to affect subtidal epibiota. *J*
520 *Exp Mar Biol Ecol* 248:177-190

521 Grave BH (1933) Rate of growth, age at sexual maturity, and duration of life of certain
522 sessile organisms, at Woods Hole, Massachusetts. *Biol Bull* 65:375-386

523 Hewitt J, Thrush S (2007) Effective long-term ecological monitoring using spatially and
524 temporally nested sampling. *Environ Monit Assess* 133:295-307

525 Johannes RE, Hearn CJ (1985) The effect of submarine groundwater discharge on nutrient
526 and salinity regimes in a coastal lagoon off Perth, Western Australia. *Estuar Coast*
527 *Shelf Sci* 21:789-800

528 Kendrick GA, Goldberg NA, Harvey ES, McDonald J (2009) Historical and contemporary
529 influence of the Leeuwin Current to the marine biota of the Southern Western
530 Australian Continental Shelf and the Recherche Archipelago. *J Roy Soc West Aust*
531 92:209-217

532 Kendrick GA, Lavery PS, Phillips JC (1999) Influence of *Ecklonia radiata* kelp canopy on
533 structure of macro-algal assemblages in Marmion Lagoon, Western Australia.
534 *Hydrobiologia* 398/399:275-283

535 Kendrick GA, Walker DI (1995) Dispersal of propagules of *Sargassum* spp. (Sargassaceae,
536 Phaeophyta) - observations of local patterns of dispersal and consequences for
537 recruitment and population structure. *J Exp Mar Biol Ecol* 192:273-288

538 Koslow JA, Pesant S, Feng M, Pearce A, Fearn P, Moore T, Matear R, Waite A (2008) The
539 effect of the Leeuwin Current on phytoplankton biomass and production off
540 Southwestern Australia. *J Geophys Res* 113

541 Langlois TJ, Radford B, Van Niel KP, Meeuwig JJ, Pearce A, Rousseaux CSG, Kendrick
542 GA, Harvey ES (2012) Consistent abundance distributions of marine fishes in an old,
543 climatically buffered, infertile seascape. *Glob Ecol Biogeogr* 21:886-897

544 Levin SA (1992) The problem of pattern and scale in ecology. *Ecology* 73:1943-1967

545 Lourey MJ, Dunn JR, Waring J (2006) A mixed-layer nutrient climatology of Leeuwin
546 Current and Western Australian shelf waters: seasonal nutrient dynamics and
547 biomass. *J Mar Syst* 59:25-51

548 Moran MD (2003) Arguments for rejecting the sequential Bonferroni in ecological studies.
549 *Oikos* 100:403-405

550 Morrisey DJ, Underwood AJ, Howitt L, Stark JS (1992) Temporal variation in soft-sediment
551 benthos. *J Exp Mar Biol Ecol* 164:233-245

552 Mullineaux LS, Butman CA (1990) Recruitment of encrusting benthic invertebrates in
553 boundary-layer flows: a deep-water experiment on Cross Seamount. *Limnol Oceanogr*
554 35:409-423

555 O'Leary J, Potts D (2011) Using hierarchical sampling to understand scales of spatial
556 variation in early coral recruitment. *Coral Reefs* 30:1013-1023

557 Paine RT, Vadas RL (1969) The effects of grazing by sea urchins, *Strongylocentrotus* spp.,
558 on benthic algal populations. *Limnol Oceanogr* 14:710-719

559 Pearce AF (1991) Eastern boundary currents of the southern hemisphere. *J Roy Soc West*
560 *Aust* 74:35-45

561 Phillips JA (2001) Marine macroalgal biodiversity hotspots: why is there high species
562 richness and endemism in southern Australian marine benthic flora? *Biodiversity*
563 *Conserv* 10:1555-1577

564 Qui JW, Qian PY (1997) Combined effects of salinity, temperature and food on early
565 development of the polychaete *Hydroides elegans*. *Mar Ecol Prog Ser* 152:79-88

566 Ritter C, Montagna PA, Applebaum S (2005) Short-term succession dynamics of
567 macrobenthos in a salinity-stressed estuary. *J Exp Mar Biol Ecol* 323:57-69

568 Rodríguez SR, Ojeda FP, Inestrosa NC (1993) Settlement of benthic marine invertebrates.
569 *Mar Ecol Prog Ser* 97:193-207

570 Schiel DR, Foster MS (1986) The structure of subtidal algal stands in temperate waters.
571 *Oceanogr Mar Biol Ann Rev* 24:265-307

572 Searle DJ, Semeniuk V (1985) The natural sectors of the inner Rottneest Shelf coast adjoining
573 the Swan Coastal Plain. *J Roy Soc West Aus* 67:116-136

574 Smale DA (2012) Extreme spatial variability in sessile assemblage development in subtidal
575 habitats off southwest Australia (southeast Indian Ocean). *J Exp Mar Biol Ecol*
576 438:76-83

577 Smale DA, Kendrick GA, Wernberg T (2010) Assemblage turnover and taxonomic
578 sufficiency of subtidal macroalgae at multiple spatial scales. *J Exp Mar Biol Ecol*
579 384:76-86

580 Smale DA, Langlois TJ, Kendrick GA, Meeuwig JJ, Harvey ES (2011a) From fronds to fish:
581 the use of indicators for ecological monitoring in marine benthic ecosystems, with
582 particular reference to the temperate nearshore system of Western Australia. *Rev Fish*
583 *Biol Fish* 21:311-337

584 Smale DA, Wernberg T (2009) Satellite-derived SST data as a proxy for water temperature in
585 nearshore benthic ecology. *Mar Ecol Prog Ser* 387:27-37

586 Smale DA, Wernberg T, Kendrick GA (2011b) Subtidal macroalgal richness, diversity and
587 turnover, at multiple spatial scales, along the southwestern Australian coastline. *Est*
588 *Coast Shelf Sci* 91:224-231

589 Smale DA, Wernberg T, Vance T (2011c) Community development on subtidal temperate
590 reefs: the influences of wave energy and the stochastic recruitment of a dominant
591 kelp. *Mar Biol* 158:1757–1766

592 Smith RL, Huyer A, Godfrey JS, Church JA (1991) The Leeuwin Current off Western
593 Australia. *J Phys Oceanogr* 21:323-345

594 Sousa WP (1980) The responses of a community to disturbance: The importance of
595 successional age and species' life histories. *Oecologia* 45:72-81

596 Sugden H, Lenz M, Molis M, Wahl M, Thomason JC (2008) The interaction between nutrient
597 availability and disturbance frequency on the diversity of benthic marine communities
598 on the north-east coast of England. *J Anim Ecol* 77:24-31

599 Svensson JR, Lindegarth M, Siccha M, Lenz M, Molis M, Wahl M, Pavia H (2007)
600 Maximum species richness at intermediate frequencies of disturbance: consistency
601 among levels of productivity. *Ecology* 88:830-838

602 Terlizzi A, Anderson MJ, Fraschetti S, Benedetti-Cecchi L (2007) Scales of spatial variation
603 in Mediterranean subtidal assemblages at different depths. *Mar Ecol Prog Ser* 332:25-
604 39

605 Thompson P, Waite A (2003) Phytoplankton responses to wastewater discharges at two sites
606 in Western Australia. *Mar Freshwater Res* 54:721-735

607 Tittensor DP, Mora C, Jetz W, Lotze HK, Ricard D, Berghe EV, Worm B (2010) Global
608 patterns and predictors of marine biodiversity across taxa. *Nature* 466:1098-1101

609 Todd CD, Turner SJ (1986) Ecology of intertidal and sublittoral cryptic epifaunal
610 assemblages. I. Experimental rationale and the analysis of larval settlement. *J Exp*
611 *Mar Biol Ecol* 99:199-231

612 Toohey BD, Kendrick GA, Harvey ES (2007) Disturbance and reef topography maintain high
613 local diversity in *Ecklonia radiata* kelp forests. *Oikos* 116:1618-1630

614 Underwood AJ (1990) Experiments in ecology and management: Their logics, functions and
615 interpretations. *Aust J Ecol* 15:365-389

616 Underwood AJ, Chapman MG (1996) Scales of spatial pattern of distribution of intertidal
617 invertebrates. *Oecologia* 107:212-224

618 Underwood AJ, Fairweather PG (1989) Supply-side ecology and benthic marine
619 assemblages. *Trends Ecol Evol* 4:16-20

620 Vanderklift MA, Kendrick GA (2004) Variations in abundances of herbivorous invertebrates
621 in temperate subtidal rocky reef habitats. *Mar Freshwater Res* 55:93-103

622 Wahl M (2001) Small scale variability of benthic assemblages: biogenic neighborhood
623 effects. *J Exp Mar Biol Ecol* 258:101-114

624 Wernberg T, Coleman M, Fairhead A, Miller S, Thomsen M (2003a) Morphology of
625 *Ecklonia radiata* (Phaeophyta: Laminariales) along its geographic distribution in
626 south-western Australia and Australasia. *Mar Biol* 143:47-55

627 Wernberg T, Kendrick GA, Phillips JC (2003b) Regional differences in kelp-associated algal
628 assemblages on temperate limestone reefs in south-western Australia. *Divers Distrib*
629 9:427-441

630 Wernberg T, Kendrick GA, Toohey BD (2005) Modification of the physical environment by
631 an *Ecklonia radiata* (Laminariales) canopy and its implications to associated foliose
632 algae. *Aquat Ecol* 39:419-430

633 Wernberg T, Smale DA, Tuya F, Thomsen MS, Langlois TJ, de Bettignies T, Bennett S,
634 Rousseaux CS (2012) An extreme climatic event alters marine ecosystem structure in
635 a global biodiversity hotspot. *Nature Clim Change* in press

- 636 Wernberg T, White M, Vanderklift MA (2008) Population structure of turbinid gastropods on
637 wave-exposed subtidal reefs: effects of density, body size and algae on grazing
638 behaviour. *Mar Ecol Prog Ser* 362:169-179
- 639 Wilson JH, Simons J (1985) Gametogenesis and breeding of *Ostrea edulis* on the west coast
640 of Ireland. *Aquaculture* 46:307-321
- 641 Witman JD, Etter RJ, Smith F (2004) The relationship between regional and local species
642 diversity in marine benthic communities: a global perspective. *Proc Nat Acad Sci*
643 USA 101:15664-15669
- 644
- 645
- 646

647 Table 1. Results of multivariate PERMANOVA to test for differences between months ('mo',
648 fixed), locations ('lo', random), sites ('si', random and nested within locations) and rings
649 ('ri', random and nested within sites). Permutations were based on a Bray-Curtis similarity
650 matrix generated from square-root transformed percent cover data. All main tests used a
651 maximum of 999 permutations under a reduced model. Significant *P* values (at <0.05) are in
652 bold.

653

654 Source	<i>df</i>	SS	MS	F	<i>P</i>
655 Mo	2	12875	6437.6	1.96	0.142
656 Lo	1	8913.9	8913.9	4.95	0.335
657 Si(Lo)	2	3595.5	1797.7	3.57	0.001
658 Mo x Lo	2	6537.2	3268.6	1.33	0.271
659 Mo x Si(Lo)	12	6042.3	503.53	4.85	0.001
660 Total	23	47749			

661

662

663 Table 2. Results of PERMDISP test to examine differences in multivariate dispersion
 664 between sampling periods (i.e. between levels of the ‘month’ factor), for each location.
 665 Degrees of freedom used were $F_{2,65}$ for Marmion Marine Park and $F_{2,69}$ for Jurien Bay,
 666 significant P values (at <0.05) are in bold. Also shown are mean distances (\pm SE) between
 667 centroids for each sampling period.

668

669	Location	F	P	3 mo	9 mo	14 mo
670	Marmion	6.07	0.009	26.3 \pm 1.4	33.1 \pm 1.3	29.2 \pm 1.4
671	Jurien	15.85	0.001	37.8 \pm 1.3	46.3 \pm 1.3	46.4 \pm 1.2

672

Table 3. Results of PERMANOVA tests to examine differences in ecological structure between locations ('lo', random), sites ('si', random and nested within locations) and rings ('ri', random and nested within sites) at each sampling period, using a fully nested hierarchical design. For multivariate assemblage structure, permutations were based on a Bray-Curtis similarity matrix generated from square-root transformed percent cover data. For all other univariate responses (i.e. total cover, taxon richness and the cover of 4 dominant taxa), permutations were based on matrices generated from Euclidian distances between untransformed percent cover data. Tests used a maximum of 999 permutations under a reduced model. Significant *P* values (at <0.01, to account for multiple tests) are in bold.

Response variable	3 Months						9 Months						14 Months					
	Lo		Si (Lo)		Ri (Si)		Lo		Si (Lo)		Ri (Si)		Lo		Si (Lo)		Ri (Si)	
	F _{1,2}	<i>P</i>	F _{2,4}	<i>P</i>	F _{4,38}	<i>P</i>	F _{1,2}	<i>P</i>	F _{2,4}	<i>P</i>	F _{4,38}	<i>P</i>	F _{1,2}	<i>P</i>	F _{2,4}	<i>P</i>	F _{4,38}	<i>P</i>
Assemblage structure	1.03	0.66	20.61	0.003	1.90	0.001	3.56	0.323	1.44	0.175	8.24	0.001	1.98	0.196	7.05	0.003	2.36	0.001
Total cover	1.26	0.368	1.17	0.386	6.57	0.001	176.3	0.009	0.30	0.825	3.84	0.011	4.63	0.153	0.13	0.903	2.59	0.050
Taxon richness	0.02	0.885	110.6	0.001	0.54	0.687	169.7	0.010	0.31	0.784	3.78	0.011	23.5	0.05	2.71	0.174	3.00	0.035
<i>T. moniliferum</i>	1.04	0.523	437.0	0.001	0.01	0.955	25.0	0.350	0.60	0.700	1.39	0.263	0.17	0.837	11.49	0.005	3.51	0.013
<i>Hydroides</i> sp. a	0.54	0.685	21.62	0.004	4.60	0.002	1.03	0.356	45.28	0.015	1.34	0.281	0.08	0.842	0.77	0.509	9.88	0.001
<i>Ostrea angasi</i>	1.09	0.340	8.07	0.011	10.16	0.001	0.87	0.955	4.21	0.017	8.87	0.001	0.84	0.843	84.45	0.009	0.13	0.991
<i>Anomia trigonopsis</i>	1.02	0.526	36.69	0.004	0.40	0.814	0.55	0.662	3.57	0.077	2.92	0.025	0.51	0.654	4.31	0.146	0.34	0.854
TOTAL SIGNIFICANT		0		5		4		2		0		2		0		3		2

FIGURES

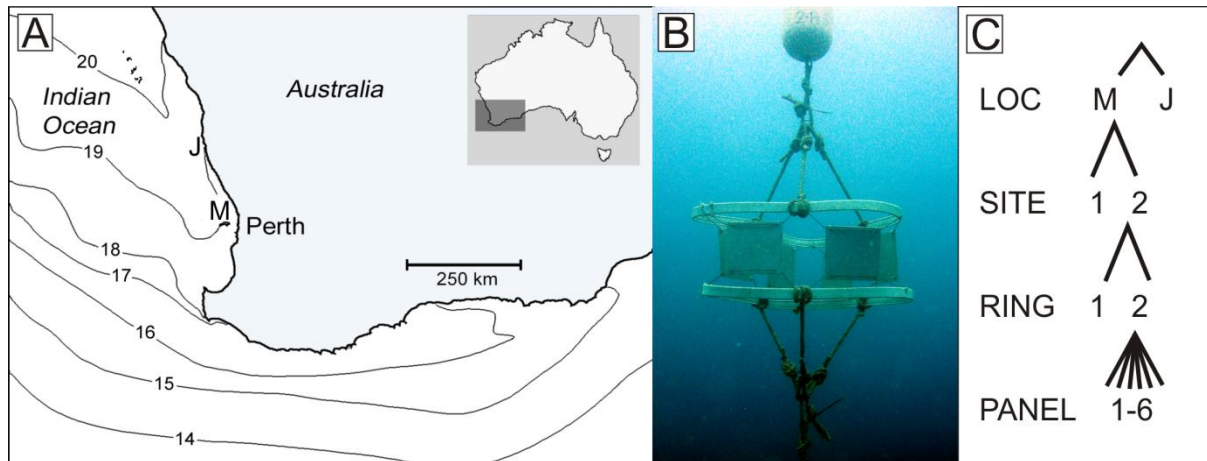


Fig. 1. (A) The position of the Marmion Marine Park (M) and Jurien Bay (J) study locations on the coastline of southwest Australia. Average winter isotherms (SSTs in °C, 2005-07) for the region are also shown. (B) A settlement panel ring *in situ*, at ~13 m depth in a mixed-substrata habitat. (C) The experimental design used to assess spatial variability at multiple scales (see methods for further details).

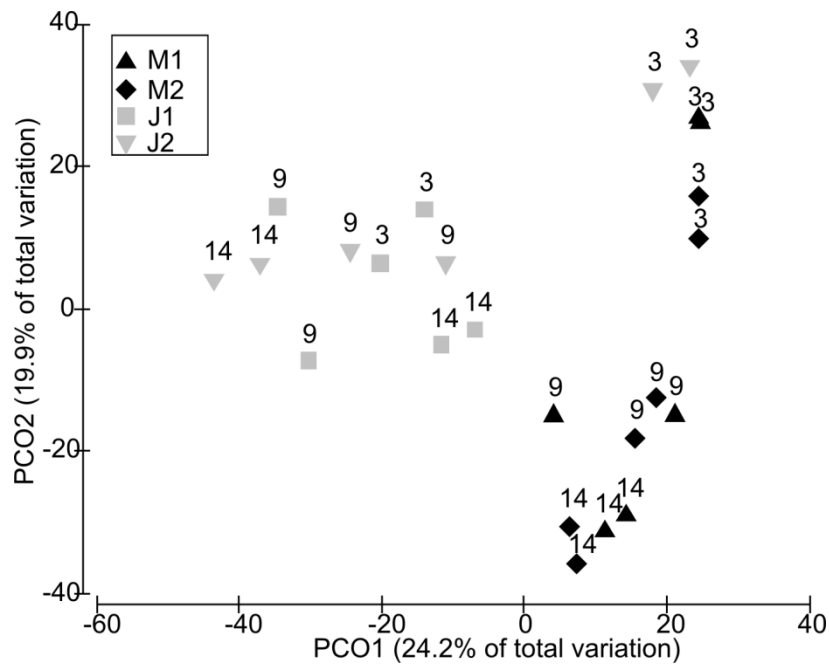


Fig. 2. PCO ordination of panel assemblages based on a Bray-Curtis similarity matrix generated from square-root transformed percent cover data. Centroids represent each ring (6 panels pooled), with 2 rings per site, 2 sites nested within each location and 3 sampling periods. Centroid colours represent locations, centroid symbols represent sites, while centroid labels show assemblage development time (in months).

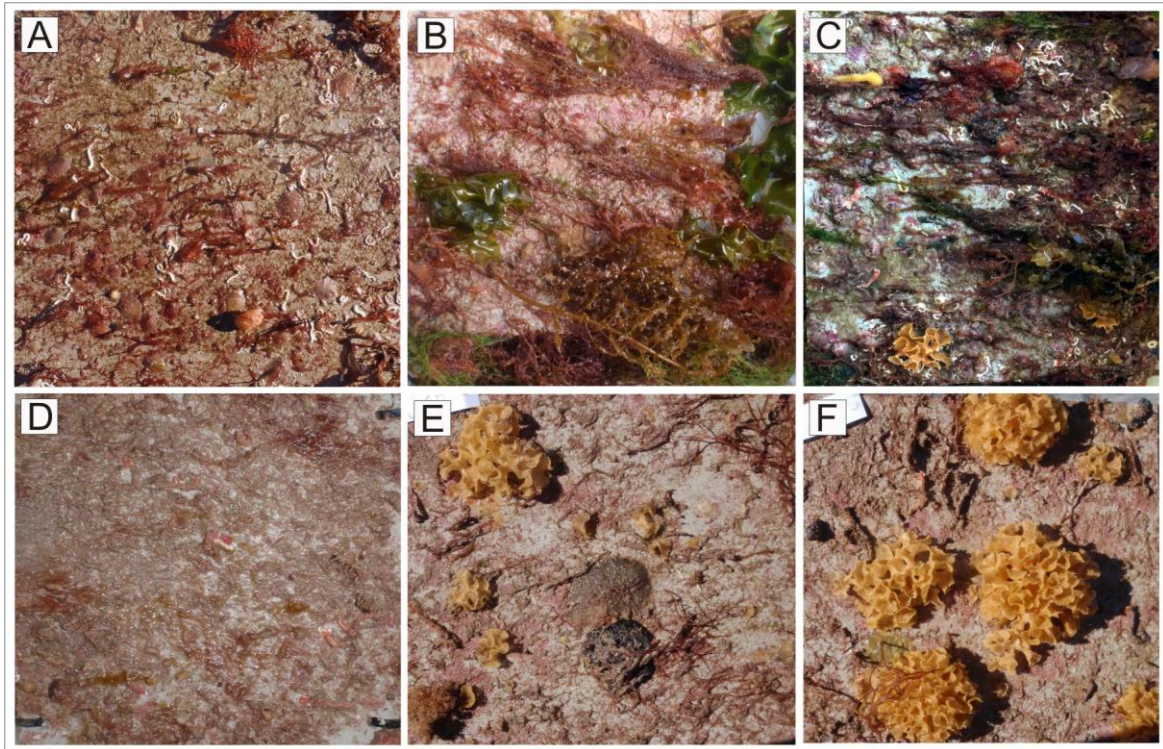


Fig. 3. Representative images to illustrate the trajectory of assemblage development at Marmion Marine Park (A-C) and Jurien Bay (D-F). At Marmion Marine Park, panels after 3 months (A) were characterised by a high cover of red macroalgae (e.g. *Spyridia dasyoides*), serpulid polychaetes (*Hydroides* spp.) and occasional bivalves (e.g. *Anomia trigonopsis*). After 9 months (B) panels were dominated by a variety of macroalgae species (e.g. *Ulva* spp. and *Sargassum* spp.), while fauna including sponges (e.g. *Scyon* spp.) and bryozoans (e.g. *Triphyllozoon moniliferum*) were more prominent in the 14 month samples. At Jurien Bay, panels were colonised by far fewer macroalgal taxa, and serpulids dominated after 3 months (D), while bivalves (e.g. *Ostrea angasi* and *Anomia trigonopsis*) and the bryozoan *Triphyllozoon moniliferum* were abundant taxa in the 9 (E) and 14 month (F) samples. Images depict an area of panel of ~160 x 160 mm.

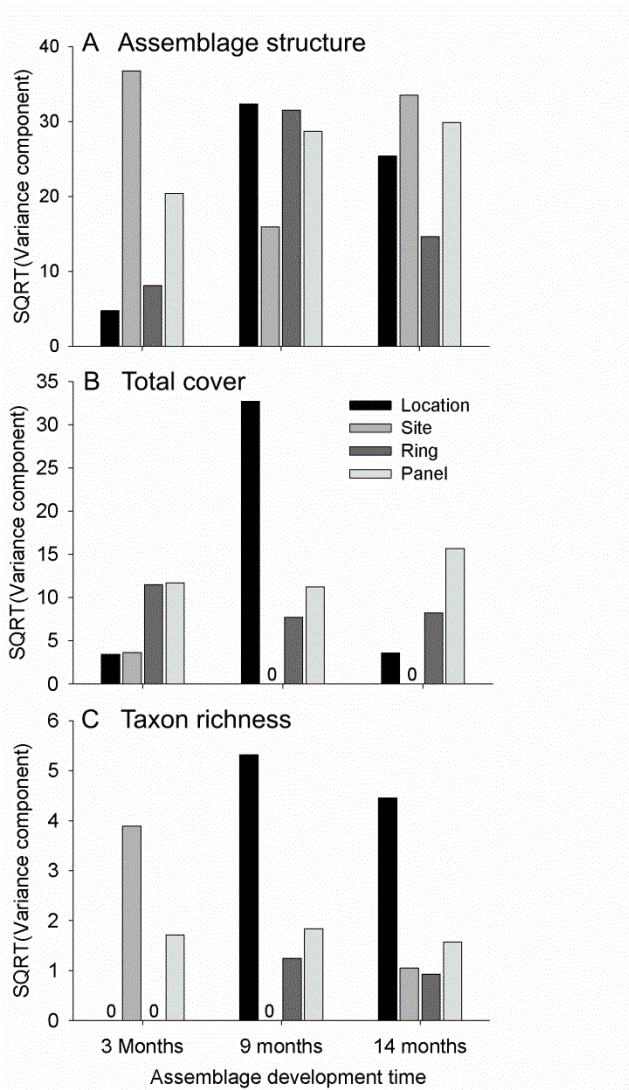


Fig. 4. Size of (pseudo) variance components for each spatial scale for variability in (A) assemblage structure, (B) total cover and (C) taxon richness, plotted against assemblage development time. Assemblage structure was based on a Bray-Curtis similarity matrix generated from square-root transformed percent cover data. Results of PERMANOVA tests are provided in Table 2.

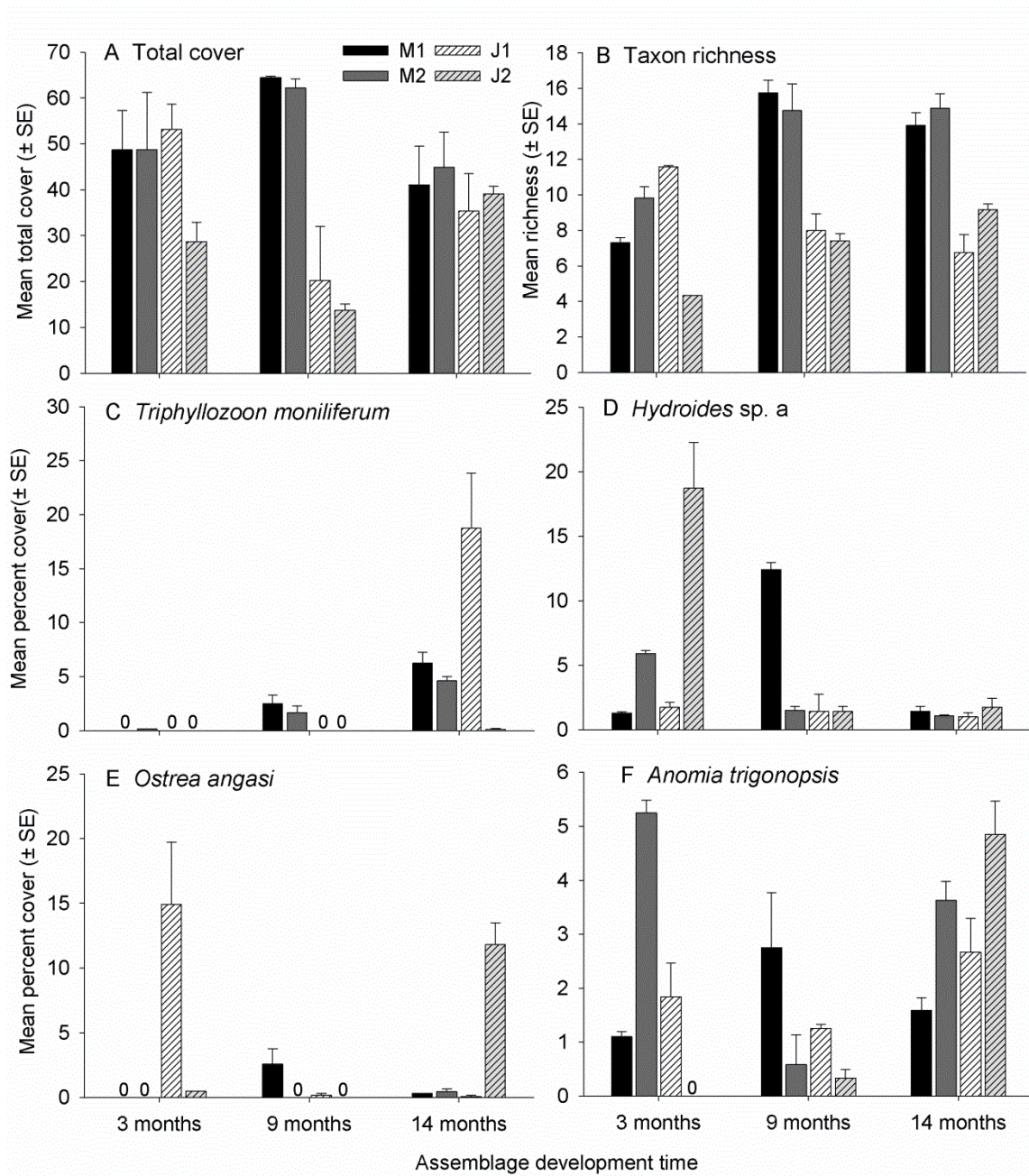


Fig. 5. Mean values (\pm SE) of total cover (A), taxon richness (B) and the percent cover of dominant taxa (C-F) at each site within each location, plotted against assemblage development time. Values are means of 2 panel rings within each site (6 panels pooled per ring). Key taxa included the bryozoan, *Triphyllozoon moniliferum* (C), the serpulid polychaete *Hydroides* sp. a (D), the oyster *Ostrea angasi* (E) and the bivalve *Anomia trigonopsis* (F). Note differences in scale between y-axes.