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

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ABSTRACT

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

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

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

INTRODUCTION

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

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

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

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

This study aimed to experimentally assess spatial variability patterns at multiple scales, from centimeters to hundreds of kilometers, in the structure of sessile assemblages across developmental stages. To achieve this goal, settlement panels were deployed in subtidal habitats off southwest Australia, which is a global hotspot of marine biodiversity and endemism (Phillips 2001, Tittensor et al. 2010), but relatively poorly understood in terms of early-stage benthic community dynamics (Smale et al. 2011a). The shelf waters off southwest Australia are strongly influenced by the Leeuwin Current (LC), which originates in the Indo-Pacific and flows polewards along the coast of Western Australia, before deviating eastwards into the Great Australian Bight (Pearce 1991, Smith et al. 1991). The LC transports tropical (and subtropical) dispersal stages and warm, nutrient-poor water polewards, which enhances north to south mixing of species and effectively raises winter water temperatures (Ayvazian & Hyndes 1995, Caputi et al. 1996, Smale & Wernberg 2009). Here, sessile assemblages were cultivated in comparatively pristine reef-dominated habitats with minimal human impact (i.e. relative to embayments and harbours) to examine 'natural' patterns of spatial variability in relation to assemblage development time.

This study tested 3 hypotheses. First, that the magnitude of variability at large spatial scales would increase with assemblage development time. This is because the structure of mature, subtidal reef assemblages is known to vary at scales of 100s of km along the southwest Australian coastline (Wernberg et al. 2003b, Smale et al. 2010). This variability is, at least in part, driven by a well-defined regional-scale temperature gradient (Smale & Wernberg 2009) that influences the local species pool and promotes sequential turnover in assemblage structure along the coastline (Wernberg et al. 2003b, Smale et al. 2010). However, as the coastline is well-connected through oceanography and other key environmental variables (e.g. primary productivity, habitat availability, wave exposure) remain relatively constant across the region (Pearce 1991, Smale & Wernberg 2009), some cosmopolitan species exhibit extensive geographical distributions (e.g. the common kelp *Ecklonia radiata*, see Wernberg et al. 2003a). Thus, it is hypothesized that early-stage assemblages will be characterized by widespread 'pioneer' species that are common to local species pools separated by 100s km. As assemblages mature, more species 'unique' to the local pool will colonize the artificial habitat, so that the magnitude of large-scale variability increases with time. The second hypothesis is that variability at the smallest spatial scales, centimeters to meters, will be consistently high regardless of assemblage development time, because variability driven by abiotic and biotic forces acting at these scales is a ubiquitous feature of marine benthic assemblages, regardless of assemblage maturity (Fraschetti et al. 2005). The third hypothesis is that patterns of spatio-temporal variability will differ between dominant taxa. Previous research has shown that, even when different species perform similar functions, variability patterns can alter markedly between species because of (sometimes subtle) differences in life histories, which consequently influence successional patterns (e.g. Benedetti-Cecchi 2000, Anderson et al. 2005). In the context of the current study, sessile species of pioneer flora and fauna were predicted to exhibit different spatio-temporal variability patterns because of dissimilarities in life histories, geographical distributions and population structures.

MATERIALS AND METHODS

Study locations

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

Experimental design

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

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

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

Analysis

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

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

‘Site’). Permutations were based on a Bray-Curtis similarity matrix generated from square-root transformed percent cover data; the transformation was used to down-weight the influence of large space occupiers. Tests used up to 4999 permutations under a reduced model and significance was accepted at $P < 0.05$. A PCO plot based on the Bray-Curtis similarity matrix was used to visualize shifts in multivariate structure through time and space. To investigate the influence of development time on spatial variability further, differences between spatial scales were examined for each sampling period (i.e. 3, 9 and 14 months) using a fully nested hierarchal design (i.e. ‘Location’, ‘Site’ and ‘Ring’, all random and spatially nested). As fully nested sampling designs provide biased and independent assessments of variability across multiple spatial scales (Underwood & Chapman 1996) this approach allowed (pseudo) variance components to be compared between spatial scales and across sampling periods. Where negative various components were generated, they were re-set to zero (Benedetti-Cecchi 2001). Variability in univariate metrics, including total cover, taxon richness and the cover of dominant taxa, was also tested with PERMANOVA, using the model described above (but with matrices based on Euclidean distances of untransformed data, which is analogous to traditional ANOVA). As many statistical tests were conducted, the probability of falsely rejecting at least one null hypothesis would have been greater than the conventional alpha value of 0.05. Rather than employ sequential Bonferroni corrections, which may be overcautious and impractical for this type of study (Moran 2003), variability was deemed significant at $P \leq 0.01$ to reduce the risk of Type 1 error. Even so, conducting >20 sequential tests increases the chance of Type 1 error and, as such, the tests were used to examine general variability patterns across sampling times and taxa, rather than generating specific significance values. Finally, for each location differences in multivariate dispersion within sampling periods was tested with PERMDISP, which essentially tests for homogeneity of variance across levels of a given factor (in this case ‘Month’). All analysis was conducted with PRIMER 6 (Clarke & Warwick 2001), using the PERMANOVA add-on (Anderson et al. 2008).

RESULTS

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

Patterns of multi-scale spatial variability were subsequently examined separately for each month with PERMANOVA. For multivariate assemblage structure, between-location (i.e. 100s km) variability was non-significant for all months, whereas significant between-ring variability (i.e. meters) was recorded for all months. Significant variability at the intermediate scale of site (i.e. ~1 km) was also recorded at 3 and 9 months (Table 3). Examination of the pseudo-variance components generated from the PERMANOVA model indicated no clear pattern in the contribution of variance components to total variability over time, although large-scale variability was markedly low for immature 3 month old assemblages (Fig. 4A). Variability at the smallest spatial scale, (i.e. between panels, ~20 cm apart) was consistently a principal source of spatial variability (Fig. 4A).

Patterns of spatial variability for assemblage-level univariate metrics (i.e. total cover and taxon richness) were similarly inconsistent through time (Table 3, Fig. 4B&C). Total cover varied significantly only at the smallest scale of ring after 3 months and the largest scale of location after 9 months (Table 3). This was also reflected in the pseudo-variance components, as variability at the smallest scales of ring and panel were major contributors to total variability, whilst variability between locations was only prominent for the 9 month samples (Fig. 4B). Plots of mean total cover for each site showed that total cover was considerably greater at Marmion Marine Park after 9 months, but not after 3 or 14 months (Fig. 5A). Taxon richness varied significantly only at the scale of site after 3 months and at the scale of location after 9 months (Table 3). This was clearly reflected in the pseudo-variance components, as variability at the scale of site was pronounced after 3 months and variability between locations was prominent after 9 months (Fig. 4C). As with total cover, variability at the scale of panel was consistently a major contributor to total observed variability in taxon richness (Fig. 4C). Plots of mean taxon richness for each site showed that richness varied considerably between the sites at Jurien Bay after 3 months, and thereafter richness was markedly greater at Marmion Marine Park compared with Jurien Bay (Fig. 5B).

Spatial variability patterns were also examined for the 4 most abundant taxa (Table 3, Fig. 5C-F). The bryozoan *Triphyllozoon moniliferum* demonstrated a general increase in percent cover over time (Fig. 5C) and was a major space occupier after 14 months, covering almost 20% of available space at Jurien Bay. The cover of *T. moniliferum*, however, varied markedly between sites, so that after 14 months its spatial coverage differed by a factor of ~20 between the two sites at Jurien Bay (Fig. 5C). Indeed, significant variability in the cover of *T. moniliferum* between sites was recorded after 3 months and 14 months, but not after 9 months (Table 3). The serpulid polychaete, *Hydroides* sp. a, was sampled at every site and sampling period, being a ubiquitous component of the sessile assemblages (Fig. 5D). Significant variability in the cover of *Hydroides* sp. a was observed between sites and rings after 3 months, and rings after 14 months (Table 3). The bivalve *Ostrea angasi*, which was common at Jurien Bay, varied significantly at the scale of ring after 3 and 9 months and at the scale of site after 14 months (Fig. 5E, Table 3). Finally, the bivalve *Anomia trigonopsis*, which was common at both locations, varied significantly among sites after 3 months (Fig. 5F, Table 3). In general, taxon-specific spatial variability patterns were largely inconsistent between taxa and showed no clear trend through time. However, significant variability was recorded more often after 3 months, compared with 9 and 14 months, and significant variability at intermediate to small spatial scales (i.e. site and ring) was recorded more often than at the largest scale of location (Table 3).

DISCUSSION

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

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

The magnitude of large-scale variability did not, however, increase predictably with development time but instead peaked after 9 months when between-location variability in assemblage structure, total cover and taxon richness was the major contributor to total variability. As 9 month panel assemblages were harvested towards the end of the austral winter, whereas 3 and 14 month assemblages were harvested in late summer, localised seasonal influences may have promoted between-location variability. For example, at Marmion Marine Park total cover and taxon richness peaked after 9 months, being significantly greater than at Jurien Bay. While Marmion Marine Park is relatively unimpacted by human activities and nutrient levels are low compared with many other temperate coastal systems (Lourey et al. 2006), the Perth Metropolitan Area (1.7 million inhabitants) sprawls northwards along the bounding coastline so that anthropogenic influences are likely to be substantially greater than at Jurien Bay (1500 inhabitants). It could be that increased nutrient levels through the winter rainy season, as a result of terrestrial run-off (Lourey et al. 2006), sediment resuspension during storms (Lourey et al. 2006), groundwater discharge (Johannes & Hearnes 1985) or effluent outlets (Thompson & Waite 2003), promoted macroalgal growth on panels in Marmion but not in Jurien, thereby creating seasonality in the magnitude of variability between locations. Repeating these experiments with initial panel deployments in different seasons would elucidate the degree of seasonality in patterns of multi-scale spatial variability with assemblage development time.

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

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

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

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

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

The final hypothesis was supported as spatial variability patterns differed between dominant species, presumably due to different life history characteristics, from timing of reproduction through to growth and competitive ability (Butler 1986, Glasby 1998, Benedetti-Cecchi et al. 2001). After 3 months, however, all species varied significantly between sites, again 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

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

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

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

Source	*df*	SS	MS	F	*P*
Mo	2	12875	6437.6	1.96	0.142
Lo	1	8913.9	8913.9	4.95	0.335
Si(Lo)	2	3595.5	1797.7	3.57	**0.001**
Mo x Lo	2	6537.2	3268.6	1.33	0.271
Mo x Si(Lo)	12	6042.3	503.53	4.85	**0.001**
Total	23	47749			

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

Location	F	*P*	3 mo	9 mo	14 mo
Marmion	6.07	**0.009**	26.3 ± 1.4	33.1± 1.3	29.2 ± 1.4
Jurien	15.85	**0.001**	37.8 ± 1.3	46.3 ± 1.3	46.4 ± 1.2

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 hierarchal 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.

	3 Months						9 Months						14 Months					
Response variable	Lo		Si (Lo)		Ri (Si)		Lo		Si (Lo)		Ri (Si)		Lo		Si (Lo)		Ri (Si)	
	$F_{1,2}$	*P*	$F_{2,4}$	*P*	$F_{4,38}$	*P*	$F_{1,2}$	*P*	$F_{2,4}$	*P*	$F_{4,38}$	*P*	$F_{1,2}$	*P*	$F_{2,4}$	*P*	$F_{4,38}$	*P*
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
T. moniliferum	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
Hydroides 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**
Ostrea angasi	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
Anomia trigonopsis	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

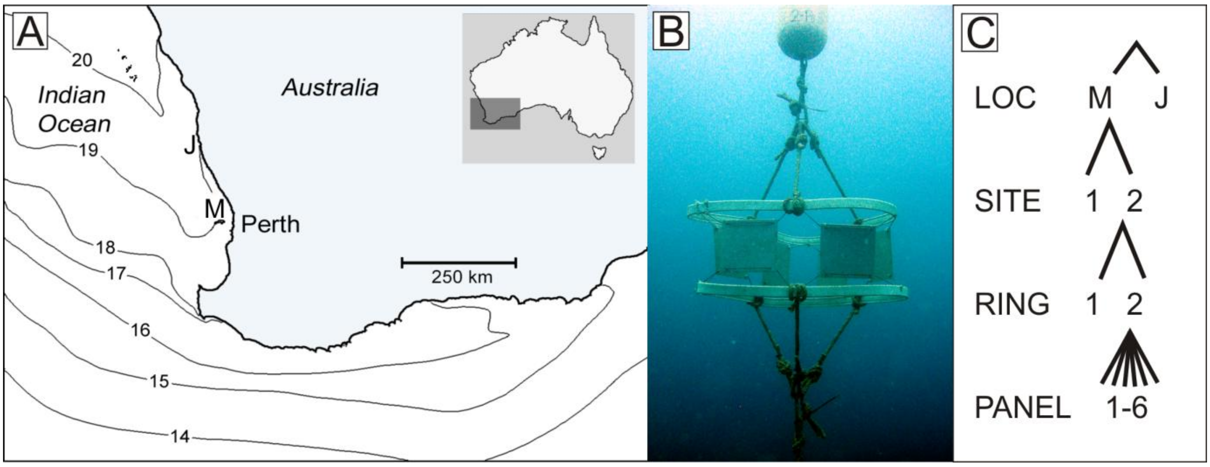

Fig. 1. (A) The position of the Marmion Marine Park (M) and Jurien Bay (J) study locations on the coastline of southwest Australia. Average winter isotherms (SSTs in °C, 2005-07) for the region are also shown. (B) A settlement panel ring *in situ*, at ~13 m depth in a mixed-substrata habitat. (C) The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

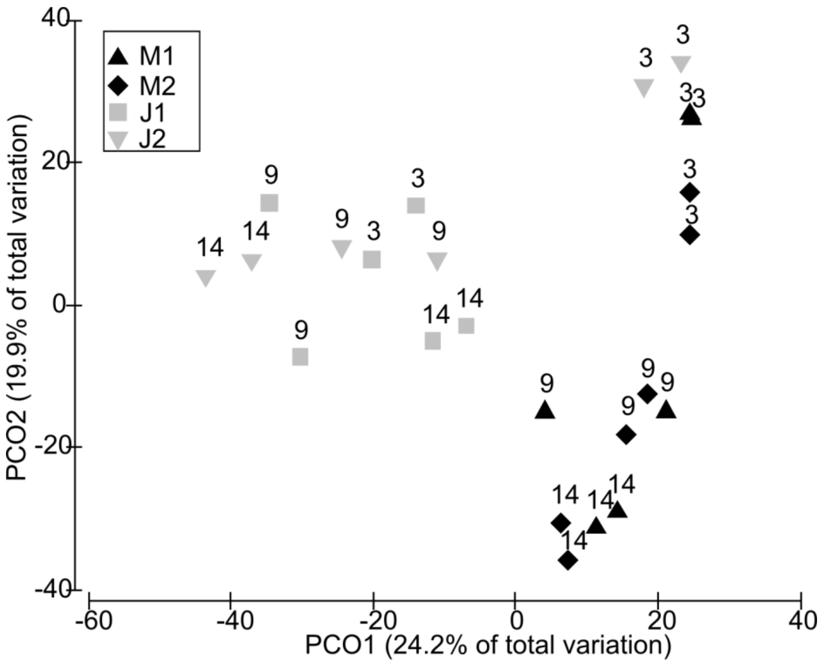

Fig. 2. PCO ordination of panel assemblages based on a Bray-Curtis similarity matrix generated from square-root transformed percent cover data. Centroids represent each ring (6 panels pooled), with 2 rings per site, 2 sites nested within each location and 3 sampling periods. Centroid colours represent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

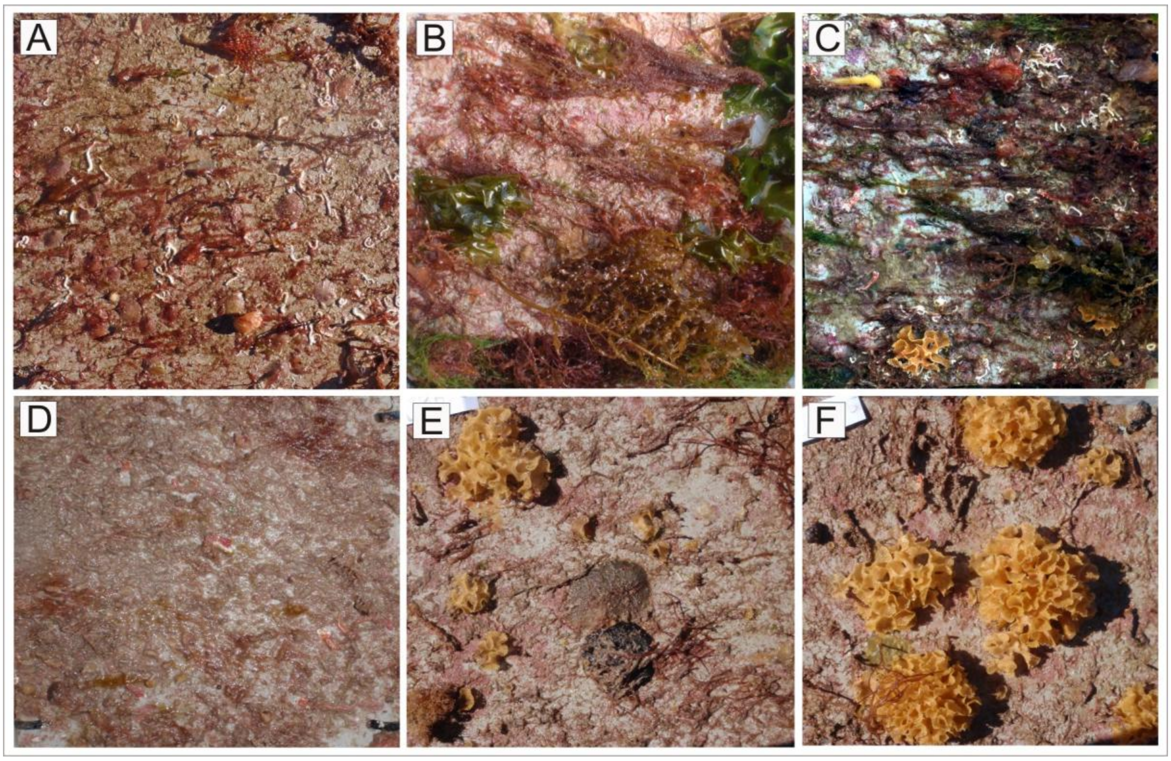

Fig. 3. Representative images to illustrate the trajectory of assemblage development at Marmion Marine Park (A-C) and Jurien Bay (D-F). At Marmion Marine Park, panels after 3 months (A) were characterised by a high cover of red macroalgae (e.g. *Spyridia dasyoides*), serpulid polychaetes (*Hydroides* 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.

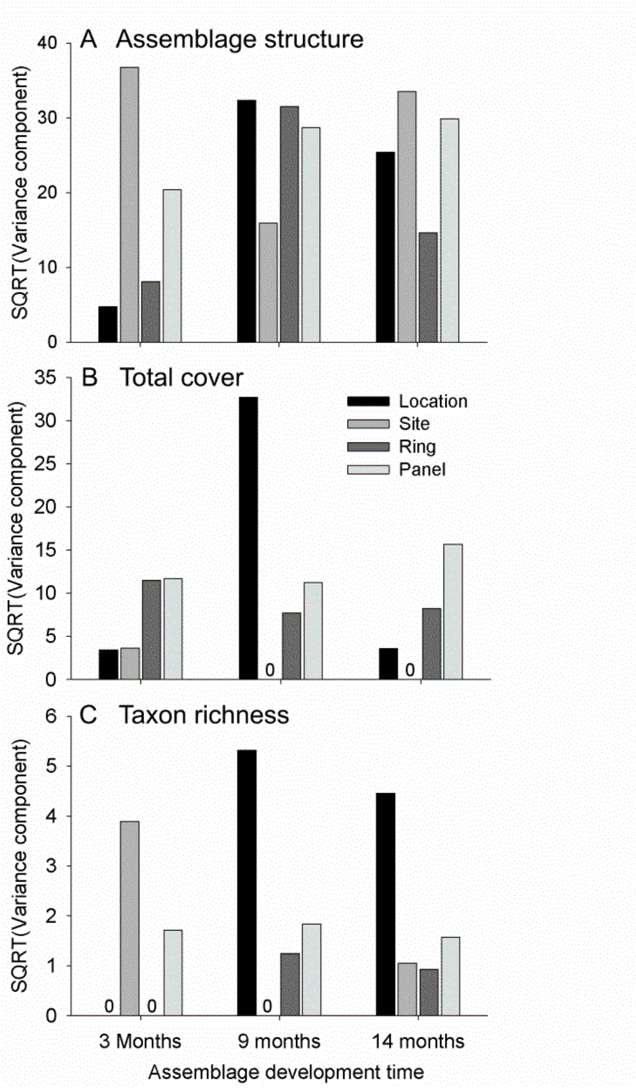

Fig. 4. Size of (pseudo) variance components for each spatial scale for variability in (A) assemblage structure, (B) total cover and (C) taxon richness, plotted against assemblage development time. Assemblage structure was based on a Bray-Curtis similarity matrix generated from square-root transformed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

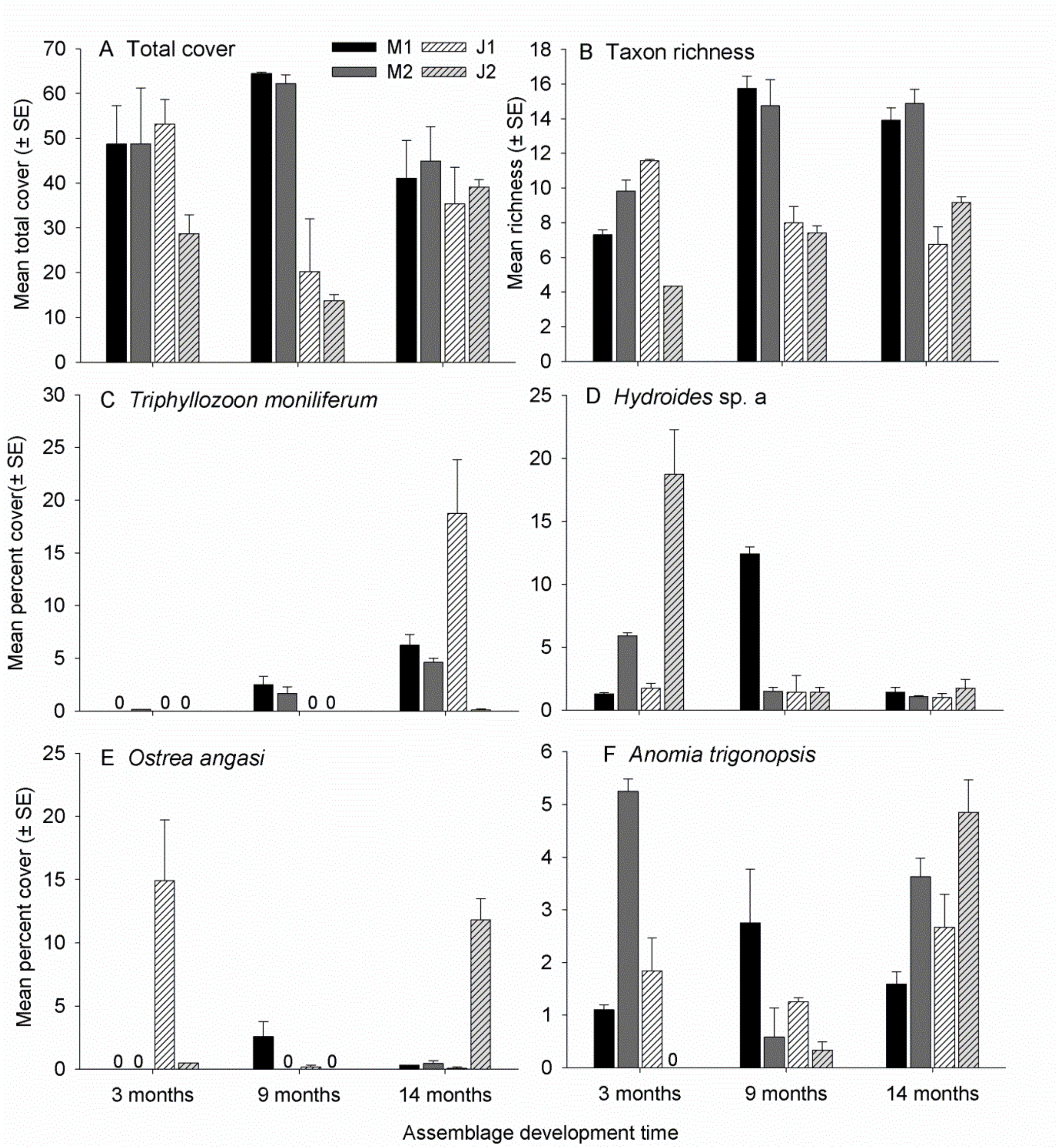

Fig. 5. Mean values (±SE) of total cover (A), taxon richness (B) and the percent cover of dominant taxa (C-F) at each site within each location, plotted against assemblage development time. Values are means of 2 panel rings within each site (6 panels pooled per ring). Key taxa included the bryozoan, *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.