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Early development of subtidal macrofaunal assemblages: relationships to period and timing of colonization

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Abstract

Colonization and successional development of very diverse subtidal assemblages on rocky surfaces are not clearly understood. Artificial units of habitat (AUHs) made of nylon pot-scourers were used to test predictions from various models of succession. An experiment was designed in an attempt to unconfound the period of deployment (equals age of succession) from the time-period during which AUHs were deployed. AUHs were deployed in two sites, 100 m apart, for 1 month, starting at 0, 1, 2 and 3 months, for 2 months, starting 0 and 2 months and for 4 months from 0 month. Ninety-nine taxa were recorded in the AUHs. Successional change was not due to nett accumulation of taxa, nor simply to longer-term AUHs sampling successive different periods of time. Assemblages developing over the same period were different, but only a small amount of the variability was seasonal. Assemblages converged as period of deployment increased. There was less change from one to two months than from two to four months in the development of assemblages, but some of this was due to seasonal difference between the first and last two months. There were no differences between sites in any of the analyses of structure of assemblages. Few individual taxa showed consistent patterns of changing abundance with length of deployment. Different types of organisms showed markedly different patterns of arrival. The increase in number of species of gastropods was much smaller than the corresponding increase in number of taxa of polychaetes. Succession in these assemblages is complex and variable, but shows some repeated patterns. Fitting these to models of succession is only partially successful and new models are needed for very diverse assemblages.
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1. Introduction

Assemblages of many types of invertebrates are found in marine, shallow-water habitats, such as in sediments (Morrisey et al., 1992a; Warwick, 1988), amongst foliose algae (e.g. Dean and Connell, 1987; Edgar and Klumpp, 2003), in mussel-beds (Suchanek, 1985; Lohse, 1993) and kelp holdfasts (e.g. Moore, 1971, 1973; Smith, 1996). They are diverse, consisting of species from many Phyla. Despite being common throughout the coastal regions of the world and in many types of habitat, the processes structuring complex infaunal assemblages or those in complex patchy habitats are not yet well understood. These assemblages are, however, often extremely patchy at small spatial scales and they vary in structure over short time-scales

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(e.g. Morrisey et al., 1992a; Thrush et al., 1994). The consequence is that assemblages are changing in composition as a result of ecological processes of recruitment and in response to disturbances (Thrush and Dayton, 2002).

Some of the major models about processes leading to temporal changes in assemblages, i.e. succession, were contrasted in a review by Connell and Slatyer (1977). In principle, processes of colonization (i.e. the arrivals of species in a patch of new habitat) are from early-colonizing species, with certain features of life-history and having particular ecological influences after they arrived, to late-colonizing species. The latter have different trends of dispersal or life-history. Different processes of succession would occur according to the types of and interactions between "early" and "late" species in any particular habitat. Note that, in all discussions of succession, observations can only be made on species that stay in the habitat long enough to be observed. Thus, analysing successional change is the analysis of nett changes, i.e. arrivals minus departures (or colonization minus extinction).

This review has been expanded and updated to consider establishment of an assemblage after a disturbance that only partially removes the previous inhabitants (Platt and Connell, 2003). This type of disturbance is probably more common than disturbances that remove everything and can result in numerous types of change in surviving assemblages. As a result of that analysis, it is clear that "directional change" in assemblages, i.e. succession leading predictably from domination by "early" species to domination by "late" species is not the only possible turn of events.

Apart from the magnitude of response to any disturbance that triggers recolonization (Thrush and Dayton, 2002) and possibly succession, in sedimentary habitats, at least, there are important effects of the size of the area to be colonized (Platt and Connell, 2003) and therefore the distance from a source of colonists (e.g. Hall, 1994). As pointed out by Whitlatch et al. (1998), small patches of habitat are likely to be colonized by larval dispersal and by drifting of adults. Larger patches are more likely to be colonized only by larvae. Thus, larger patches will take longer to develop climactic assemblages. They will also probably be colonized earlier by different species, i.e. those with dispersive stages of life-history (Levin, 1984). There are numerous other influences, including for marine assemblages, dependence on which species happen to colonize first (Sutherland and Karlson, 1977; Dean and Hurd, 1980) and the indirect effects of consumers, which influence the outcome of interactions for space (Russ, 1980; Hixon and Brostoff, 1996). The processes leading to a recognizable structure (the types and relative abundances of species) in an assemblage are therefore complex and interactive.

Turfing and other mat-like habitats are widespread in inter- and subtidal habitats. They contain numerous invertebrates, in association with the habitats themselves or with the sediment they trap. They are colonized within a few months (Dean and Connell, 1987; Myers and Southgate, 1980; Kelaher, 2005). There have, however, been very few studies of patterns or processes of colonization of these habitats in relation to temporal succession or spatial variation.

One of the problems encountered in unravelling development of assemblages in complex coastal habitats is the great variability in time and space routinely encountered (e.g. Myers and Southgate, 1980; Morrisey et al., 1992a,b; Kelaher, 2005). Obviously, some of this is due to variations in supply-side processes — the timing and numbers of organisms available to recruit vary considerably from time to time and place to place (e.g. Underwood and Fairweather, 1989). At the same time, there are variations in space and time in the suitability or "acceptability" of habitat (Singer, 2000) to potential colonists. Thus, the history and, in particular, history of disturbances and previous development of assemblages in pieces of habitat can vary spatially and temporally (Sutherland, 1980; Sousa, 1979a,b). These interact to make it difficult to discern patterns by sampling and description of succession. Experiments are necessary (Connell and Slatyer, 1977).

Some of the studies of related assemblages (e.g. Dean and Connell, 1987; Kelaher, 2005) used defaunated patches of habitat, with uncertain artefactual consequences for the subsequent recolonization. Others, such as Rule and Smith (2005), in contrast, used pot-scourers to examine colonization by subtidal fauna over various spatial scales and concluded that small-scale variation (scales of metres) was uncommon, but variation at larger scales (10s of m to km) was widespread. This is inconsistent with the variability at small scales shown by Kelaher (2005), but his studies were intertidal and in a different climatic region of south-eastern Australia.

The processes of colonization and succession – if indeed there is actually a proper succession in such volatile assemblages – are not clearly understood. In fact, the patterns of successional change are not yet well-documented. In the present paper, experiments were done to determine patterns (and, eventually, to be able to understand the processes involved) in colonization of mobile fauna in complex habitats in subtidal areas. Artificial units of habitat (AUHs; namely, pot-scourers;

Gee and Warwick, 1996) were used to provide habitats of uniform size, complexity and history, that were devoid of fauna, but had not been defaunated. These units were chosen to remove or substantially reduce uncontrollable variation among replicates, due to differences in size, structure and composition of patches of habitat, previous history of disturbances or previous colonization.

Various models of colonization were investigated here, in order to provide a base for future examination of the most relevant processes. These were about two aspects of colonization: the extent to which succession is developed by the nett addition of species, i.e. an increase in number of species present through time and the degree to which development of assemblages is consistent in time and place. This is consistent with other authors' usage — the number of species increases through time because arrivals of new species are more numerous than losses of previously arrived species. It recognizes that the number present increases as the nett change of arrivals minus departures. From published accounts, it was proposed that succession progresses because of the addition of taxa (e.g. Gwyther and Fairweather, 2002). We considered that the structure of an assemblage (composition of taxa and their relative abundances) would "stabilise" within a few (3–5) months (Dean and Connell, 1987; Myers and Southgate, 1980; Gwyther and Fairweather, 2002; Rule and Smith, 2005; Kelaher, 2005). We further proposed that the composition of fauna in later stages was simply the sum of what accumulated (i.e. no process operates to facilitate or inhibit later arrivals). As alternative models, we also considered that colonization was entirely deterministic ("Clementsian") and therefore independent of the site or time of initiation. If development of assemblages were not deterministic, we considered that assemblages should vary in their development because of variable arrivals and departures of taxa (taxonomic composition varies) or, alternatively, because similar taxa successfully colonize, but in variable relative abundances.

A particular issue in description and analyses of successional processes is that experimental studies often confound two different components of time-course in development of an assemblage. By definition, succession can only be identified when there is some consistent pattern of temporal change in the mixture or relative abundances of species present. Therefore, assemblages must be sampled after different periods of colonization. As a result, any assemblage developing for a long period (say a year) is available for colonization by species occurring or breeding in different seasons. So, any difference between assemblages after, say, 6 months and a year could be due to successional change (i.e. the result of successional development of the assemblage during the second period of six months). Alternatively, the difference could be just seasonal change — due to events occurring in the second six months which did not occur during the first six months, but would have been identified as early stages of succession if the experiment had started six months later. In an attempt to separate these two different aspect of time-course, experiments were designed to start at different times, to end at different times and to span different periods of colonization (see also, Chapman, 2002).

2. Materials and methods

2.1. Experimental design

In a pilot experiment, AUHs were deployed for three 1-month periods, two 3-month periods or one 6-month period during a 6-month experiment in two sites on subtidal reefs at the Cape Banks Marine Research Area, New South Wales, Australia. Many AUHs were lost because of severe weather and formal analyses were not done, but results indicated that the 3- and 6-month old assemblages did not differ (see Results). The pilot experiment was used to determine the appropriate taxonomic resolution for efficient sampling of assemblages and enabled us to design the main experiment.

In this experiment, one, two and four months were chosen to quantify patterns of change in the assemblage to a relatively stable point, while minimizing the total period that the experiment could be adversely affected by the weather. AUHs were deployed for one, two or four months, with 1-month, 2-month or 4-month treatments deployed at different starting times throughout the experimental period (Fig. 1).

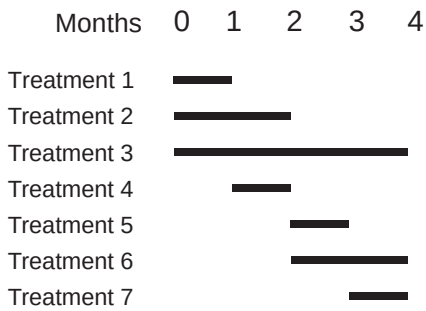

Fig. 1. Experimental design. 4 replicate AUHs were sampled for each treatment (T1–T7) which were deployed starting at 0, 1, 2 or 3 months for 1, 2, or 4 months.

2.2. Field methods

AUHs were built of commercially available plastic pot-scourers, approximately 10 cm in diameter and 3 cm thick. Each scourer was attached to a square piece of plastic foam sheet overlying a firmer compressed fibro sheet using a Cable-tie. Previous sampling had shown that collection of scourers in the field by enclosing them in a plastic bag prior to removal from the substratum, allowed animals to escape from the scourer. To prevent this, each scourer was collected inside a corer, by coring around the scourer without disturbing it, using a PVC pipe slightly larger in diameter than the scourer. This cut through the foam to the backing plate. Each corer had 63 μm mesh netting across the top surface to allow water, but not macrofauna to escape through the top of the corer. The cored section of the foam sealed the other end of the corer, with the scourer and associated assemblage inside the corer. Then a plastic bag was attached around the lower part of the corer, after animals had been brushed off the back surface of the foam plate. Each AUH therefore included animals in the scourer and between the scourer and the foam sheet, but not elsewhere on the foam sheet.

The AUHs were deployed in a sheltered bay (Long Bay, New South Wales). This area is sheltered from wave-action except in south-easterly weather. Two sites, with near-horizontal rocky ledges, were selected in 5–10 m of water, approximately 100 m apart. Sites were typical of local "Barren grounds" (Andrew, 1993; Underwood et al., 1991), i.e. extensively grazed by sea-urchins and covered by encrusting, non-geniculate coralline algae. In each site, black PVC mats (approximately 30 × 40 cm) were attached to the rock-ledges using Dynabolts to form a single grid, large enough to ensure that all AUHs were at least 10 cm apart. The replicate AUHs for each treatment were randomly allocated to positions on the grid a priori to randomize treatments across the grid and then attached to the mat with Cable-ties. No positions were used more than once, ensuring independent samples for each time. There were 4 replicates per treatment in each site.

2.3. Laboratory methods

The AUHs were preserved in 7% formal-seawater. Each scourer was then removed from the foam backing plate, unravelled and washed over a 500 μm mesh sieve, while agitating to dislodge all animals. This was added to all other animals in the sample previously dislodged from the scourer or foam. Each sample was then examined for approximate abundances of fauna. Samples with relatively few animals were sampled completely. Those with larger abundances (which were randomly scattered across times and periods of deployment) were divided into subsamples using a plankton splitter and random subsamples sorted to a maximum of 3 h per AUH. Pilot studies showed that subsampling identified a representative range of the taxa present (except for very rare taxa which do not contribute much to differences among treatments) and at the same relative abundances. Data from subsamples were multiplied to give numbers per AUH.

Taxa were identified to different taxonomic resolution, depending on relative abundances, available taxonomic expertise and the time needed to distinguish taxa. Gastropods and chitons were identified to species or morphospecies (i.e. consistently, but not formally, sensu Oliver and Beattie, 1996). Polychaetes were identified to families, with an additional category of "juveniles" for small individuals which could not be readily identified. Other taxa were grouped into larger categories (e.g. isopods, amphipods, oligochaetes, nematodes, etc.). Apart from amphipods, which could not readily be identified further, most were singletons (i.e. 1 individual in only 1 AUH). Other taxa were rare or uncommon in the samples; if added together, they contributed <5% of overall abundances. Previous work had shown similar spatial patterns in assemblages using a mix of taxonomic resolution for different groups (e.g. Chapman, 1998).

In addition, analyses of data from the pilot experiment, where finer taxonomic resolution was used (e.g. bivalves identified to species, amphipods to families) showed similar nMDS plots and identical interpretation of analyses whether fine, coarse or mixed resolution was used. Therefore, taxonomic resolution was reduced in the main experiment order to maximise the number of AUHs that could be processed with available resources.

3. Results

3.1. Model 1: older assemblages are more diverse (i.e. contain more taxa)

The hypothesis tested from this model was that the assemblage developed after one month would have fewer taxa than those in AUHs deployed for longer. Overall, there were 99 taxa, including 66 species of gastropods and 24 families of polychaetes.

This hypothesis was not supported for either the total number of taxa per treatment (summed across AUHs in each sample, Fig. 2A), nor for the mean number of taxa

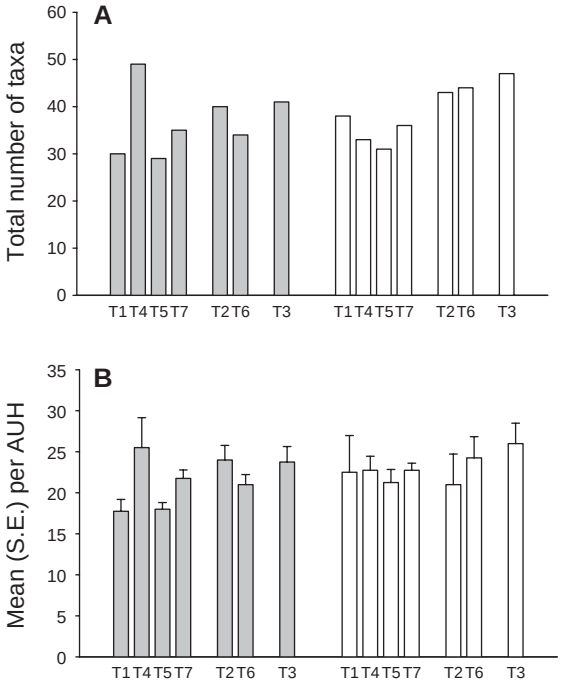

Fig. 2. (A) Total number of taxa per treatment and (B) mean (S.E.) number of taxa per AUH; T1–T7 refer to Treatments 1–7 in Fig. 1; different shadings show sites 1 and 2.

per AUH (Fig. 2B). For the total number of taxa, differences among the AUHs deployed for the same length of time were as large as differences among AUHs deployed for different amounts of time. Only between 29% (for Treatment 4, site 1) and 47% (Treatment 5, site 2) of all taxa were found in a single treatment.

The mean number of taxa per AUH was compared across all treatments and between sites using analysis of variance, but no significant differences were found (all F-ratios had $P>0.05$).

Note that the total number of species and mean number of species per treatment/site showed very similar patterns. This indicated that most species were distributed across replicates in similar ways in all treatments.

3.2. Model 2: stable assemblages develop within a few months

The hypothesis tested from this model was first examined with data from the pilot experiment. It predicted that the assemblage after three months would differ from that found after one month, but would be similar to that found after six months. As all AUHs were lost from one site and there were only two replicates of the 6-month treatment in the second site, formal analyses were not done. Treatments were compared in an nMDS plot from Bray–Curtis dissimilarities (Bray and Curtis, 1957) calculated on untransformed data (Fig. 3).

One-month assemblages were clearly different from each other and from three- and six-month assemblages, which plotted together (Fig. 3). Therefore, it appeared that the 3- and 6-month assemblages were very similar, especially when compared to younger assemblages.

In the main experiment, assemblages were compared among treatments and between sites, using npMANOVA (Anderson, 2001), again using Bray–Curtis dissimilarities on untransformed data. There was no significant effect of site ($F_{1,42}=1.55$, $P>0.05$), nor interaction between site and treatment ($F_{6,42}=0.73$, $P>0.05$), but there was a significant effect of treatments ($F_{6,6}=8.78$, $P<0.01$), showing that assemblages varied among treatments in a similar way in each site. Averaged across sites, all treatments differed significantly from all others.

Nevertheless, despite variability among the different treatments which had been deployed for the same amount of time, there were clear trends which are illustrated in nMDS plots. Assemblages changed between one and four months with similar patterns in each site. Assemblages which developed over two months were clearly intermediate between the younger and older assemblages (Fig. 4A, B).

This is also supported by the average Bray–Curtis measures (Table 1). The average dissimilarity between 1- and 2-month assemblages (within the same "season", i.e. T1 and T4 vs T2, T5 and T7 vs T3) were of similar magnitude as between replicate 1-month or replicate 2-month deployments, between 37% and 41% (Table 1).

Fig. 3. nMDS plots of assemblages in AUHs calculated from Bray–Curtis measures on untransformed data in the preliminary experiment; (●, ■, ▲, deployed for one month; ◍, ▽, deployed for three months; □, deployed for six months).

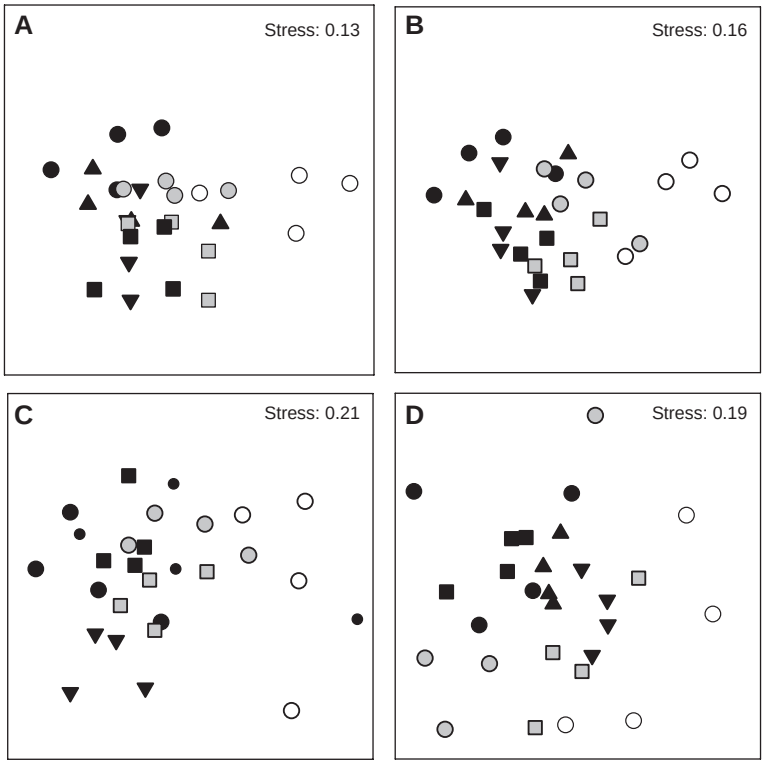

Fig. 4. nMDS plots of assemblages in (A, C) site 1 and (B, D) site 2; (A) and (B) are raw data (●, ■, ▲, ▼, Treatments 1, 4, 5 and 7, deployed for one month; ◯, ▢, Treatments 2 and 6, deployed for two months; ○, Treatment 3, deployed for four months); (C) and (D) show results from analyses of presence/absence.

Therefore, there was relatively small change in the assemblage between one and two months. There was, however, a greater change between two and four months than between one and two months, indicating that more change in the assemblage occurred in the latter part of the experimental period.

In addition to a clear change in the assemblage with longer deployment, there was also a seasonal pattern (i.e. at the temporal separation of 2 months) in the assemblage, with Treatments 1, 2 and 4 (deployed in the first two months) separating in the vertical axis from Treatments 5, 6 and 7 (deployed in the second two months). Examination of these differences – within a 2-month period vs between 2-month periods — indicated that seasonal differences were quite small relative to shorter time-intervals. Thus, the mean Bray–Curtis measures between 1-month deployments in the same 2-month period (T1 vs T4 and T5 vs T7) were 38%. Differences between 1-month deployments across a 2-month interval (i.e. T1 vs T5 and T4 vs T7) were 40% (averaged across sites from Table 1). The seasonal source of difference only contributes about 2% extra dissimilarity.

Variability among replicates within treatments was of similar magnitude for all treatments (Table 1), indicating that variability in colonization among replicates was similar, irrespective of length of deployment.

3.3. Model 3: older assemblages are simply nett accumulations of colonization and not fundamentally different assemblages

A hypothesis from this model predicted that there would be no significant difference between assemblages "constructed" from assemblages found in two consecutive periods of time (e.g. the assemblages developing between 0 and 1 month and between 1 and 2 months; i.e. T1 and T4 or T5 and T7) and the assemblage that develops in the AUHs over the complete period of time (i.e. between 0 and 2 months; T2 or T6). Similarly, that assemblages "constructed" from those developing over shorter periods throughout 4 months (Treatments 2 and 6, or from Treatments 1, 4, 5 and 7) would not be significantly different from the 4-month assemblage in Treatment 3.

Table 1
Mean percentage Bray–Curtis dissimilarity measures for comparisons within and between time-periods for AUHs deployed for one, two or four months; data averaged across all relevant pair-wise comparisons between treatments (see text for details)

Periods	Treatments	Mean dissimilarity	
		Site 1	Site 2
Within 1-month deployments	T1, T4, T5 and T7	36	32
Within 2-month deployments	T2, T6	33	33
Within 4-month deployment	T3	42	34
Between 1-month deployments within a 2-month period			
	T1 vs T4	39	38
	T5 vs T7	38	37
Between 1-month deployments across a 2-month period			
	T1 vs T5	45	40
	T4 vs T7	40	36
Between 2-month deployments across a 2-month period			
	T2 vs T6	37	41
Different periods of deployment			
1 month vs 2 months	T1, T4 vs T2; T5, T7 vs T6	37	39
2 months vs 4 months	T2, T6 vs T3	48	46
1 month vs 4 months	T1, T4, T5, T7 vs T3	58	58

All pair-wise comparisons were significantly different (npMANOVA, $P<0.05$).

These hypotheses were tested by randomly pairing AUHs from appropriate treatments to give 4 replicates of a "constructed" assemblage for T1 and T4 (to compare to T2), T5 and T7 (to compare to T6), T1, T4, T5 and T7 (to compare to T3) and T2 and T6 (to compare to T3). These assemblages were corrected for the different size of habitat caused by adding data from more than AUH by dividing each taxon by two (when two AUHs were combined) or four (when four AUHs were combined). These treatments were compared across sites, using npMANOVA for each separate comparison.

Analyses were done using raw data and, separately, after standardization (i.e. numbers of taxa as proportions of the whole assemblage). Analyses of raw data should identify differences due to differences in taxa and/or abundances. Standardization compares the relative abundances of taxa, which should not be different between the two samples if species simply accumulate in a similar pattern through time. Thus, if an assemblage developing over a 2-month period differs from that developing over a 1-month period simply by having more of every taxon, there would be a difference in analyses of raw data, but no difference using standardized data.

The natural and "constructed" assemblages were significantly different (at $P<0.01$) for all comparisons, except T5 and T7 vs T6 ($P=0.06$). Analyses of standardized data gave similar results. Therefore, assemblages do not simply change through time by the simple addition of individuals of a similar suite of species. This is clearly illustrated in Fig. 5, where the "constructed" 2-month assemblages (black symbols) clearly plot separately from the natural 2-month assemblages (grey symbols) and the "constructed" 4-month assemblage (□) plots separately from the natural 4-month assemblage (○).

For most comparisons, including analyses of raw and standardized data, the variation among replicates was larger in the natural assemblages than in the "constructed" assemblages (Table 2), which is probably a consequence of averaging to construct the latter. The differences between natural and "constructed" assemblages developing over different periods of colonization also showed an interesting pattern. The difference was a mean of 34% for the 2-month natural assemblage vs that constructed from 1-month deployments (averaged for both sets of data across both sites in Table 2). The difference between the 4-month natural assemblage and that constructed from 2-month deployments was 45% (averaged across the two sites). There was a 55% difference between the natural assemblage and that constructed from 1-month deployments.

These data show that older assemblages are not simply formed by accumulations of colonization. Thus, during the second month, animals colonized novel AUHs differently from the way that they colonized AUHs that had been deployed throughout the previous

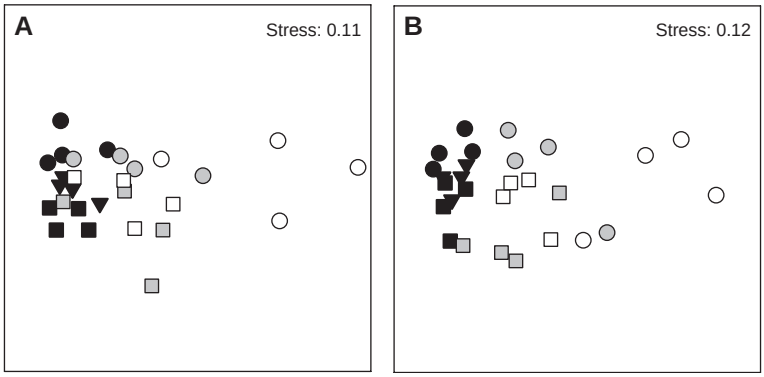

Fig. 5. nMDS plots of assemblages in (A) site 1 and (B) site 2 of natural and "constructed" assemblages (details in text); Constructed: (● — Treatment 1 and 4, ▼ — Treatments 5 and 7, ■ — Treatments 1, 4, 5 and 7, □ — Treatments 2 and 6); Natural: (◍ — Treatment 2, ▩ — Treatment 6, ○ — Treatment 3).

month. The differences were larger for the comparison of novel (1-month) and even older (4-month) AUHs.

3.4. Model 4: the rate and direction of colonization is independent of the site where and the time when the AUHs are deployed

The first hypothesis from this model was that assemblages would be independent of the site at which the AUHs were deployed. This was tested in the analysis described above for Model 2. The lack of significant interactions or effects of site showed that similar assemblages developed in all treatments between two sites approximately 100 m apart.

Table 2
Mean Bray–Curtis dissimilarity within "constructed" (C) and natural (N) and between assemblages (C vs N)

"Constructed" assemblage	Natural assemblage	Site 1			Site 2		
		C	N	C vs N	C	N	C vs N
Analysis of raw data							
1 month	2 months						
T1+T4	T2	28	31	32*	21	32	36*
T5+T7	T6	25	35	34	25	34	35
2 months	4 months						
T2+T6	T3	31	42	47*	26	34	43*
1 month	4 months						
T1, T4, T5+T7	T3	21	42	55*	18	34	55*
Analysis of standardized data							
T1+T4	T2	26	19	24*	21	25	27*
T5+T7	T6	24	30	30	24	30	32
T2+T6	T3	22	34	39*	23	29	33*
T1, T4, T5+T7	T3	19	34	42*	18	29	38*

"Constructed" assemblages are made by combining data from two sets of AUHs, each deployed for half of the time of the natural assemblage; *indicates significant differences ($P<0.01$) in npMANOVA.

There was clearly some temporal variability due to an apparent "seasonal" effect between the first and second 2-month period (Fig. 4A, B and see earlier). The two 1-month deployments in each of these "seasons" (T1 vs T4, T5 vs T7) were significantly different (npMANOVA, $P<0.05$). Mean dissimilarities between deployments were similar to those within deployments (Table 1). Similarly, assemblages in the two 2-month deployments, T2 and T6 were significantly different.

Therefore, assemblages were consistent between sites and relatively consistent among times, except when times spanned an apparent season (i.e. 2 months difference in date of deployment).

3.5. Model 5: short-term unpredictability of taxa that colonize AUHs causes greater variability in young assemblages and more apparent convergence of older assemblages

If AUHs are colonized by whichever species happen to be available when they are deployed, there will be variation among scourers deployed for the same period, but starting at different times. As more time goes by, AUHs "sample" more of the available colonists, reducing the temporal variability among deployments. One hypothesis from this model predicted that there would be larger differences among scourers deployed for 1 month, starting at different times, than among scourers deployed for 2 months, starting at different times. So, a smaller proportion of those taxa that had colonized after one month would be found in common among the four 1-month deployments than the proportion of taxa that had colonized by two months that are found in common between the two 2-month deployments.

Over all treatments and both sites, 77 taxa colonized the various 1-month AUHs; 23 (or 30%) of these were

found in all four samples (T1, T4, T5 and T7). Of the 72 taxa that were found after two months of deployment, 37 (52%) were found in both treatments (T2 and T6). There is, however, a seasonal component to this because the 1-month treatments appeared to span a season (as shown above). When similar 1-month comparisons are made within each season, there were 62 taxa in T1 and T4, of which 53% were shared and 53 taxa in T5 and T7, of which 56% were shared. Therefore, older assemblages had similar numbers of taxa and these were similarly distributed across replicates and times of deployment.

Patterns varied between taxa; 17 families of polychaetes colonized in one month, with an average of 11 over the eight AUHs deployed as one treatment over the two sites. Twenty families colonized in two months (mean = 15.5) and 17 in four months. In contrast, the species of gastropods decreased through time. Altogether, 66 species were found. Of these, 53, 46 and 34 species were in 1-month, 2-month and 4-month AUHs, respectively. The mean number in each set of eight AUHs deployed at the same time was, however, 28 for 1-month deployment, 32 for two months and 34 for four months. There were therefore very different patterns of colonization relative to the pool of species available.

These differences with period of deployment may have been influenced by the fact that the number of AUHs also decreased with period of deployment (there were 16 × 1-month, 8 × 2-month and 4 × 4-month AUHs). Throughout the entire experiment, there were always twelve AUHs deployed in each site. The total amount of habitat available for colonization in each site is 4 AUHs × 4 months for each period of deployment. If number of taxa is purely a function of how many scourers are sampled, there should be similar trends for different types of organisms and not the difference seen between polychaetes and gastropods.

3.6. Model 6: short-term unpredictability of abundances of the taxa contributes to temporal variation of assemblages

There was no greater unpredictability in the taxa colonizing one-month deployments than those colonizing two-month deployments (see previous section). Deployments for different periods of time and deployments for the same period, but starting at different times, may therefore differ because the abundances of common taxa vary from time to time or period to period.

A hypothesis from this model is that the differences among replicate deployments of the same length of time would decrease when data were analysed as presence/absence, thus minimizing any effect of variation in

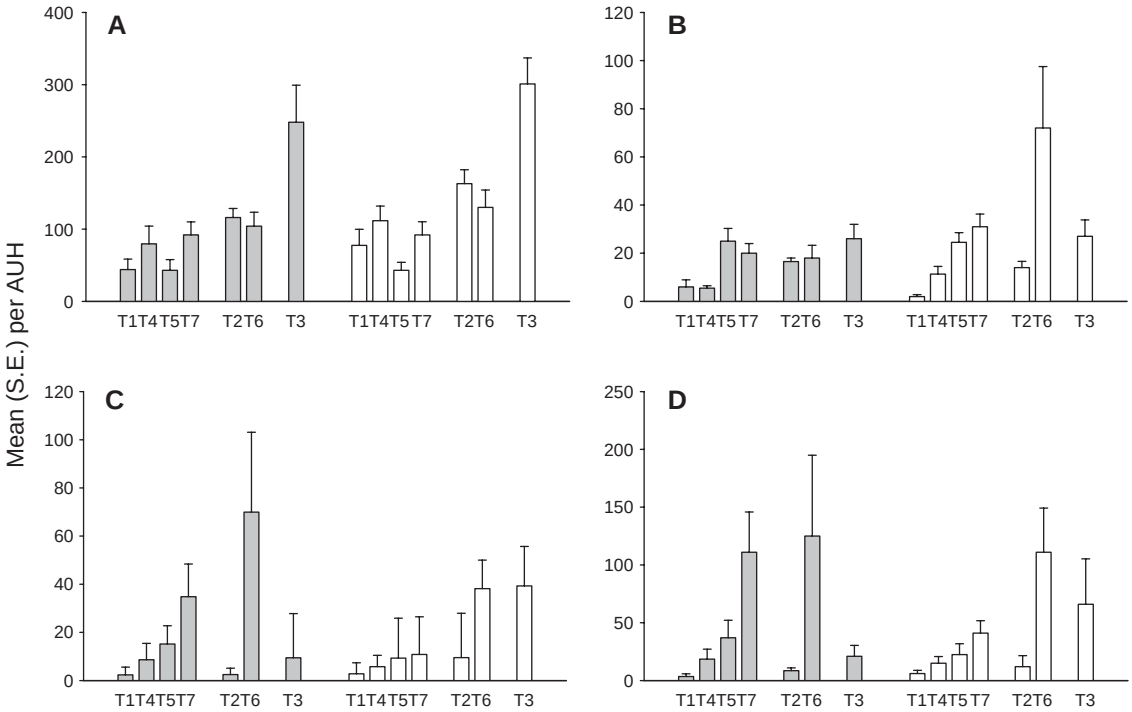

Fig. 6. Mean (S.E.) number of (A) syllid polychaetes, (B) nereidid polychaetes, (C) *Amphithalamus incidata* and (D) *Rissoella micra* per AUH in each treatment.

abundances. Although analysis of presence/absence reduced the magnitude of Bray–Curtis dissimilarities and reduced the overall patterns of difference among treatments (Fig. 4C, D compared to Fig. 4A, B), most pair-wise comparisons were still significantly different. Therefore, differences among treatments were not primarily caused by differences in abundances.

A few taxa showed less variability in mean numbers of individuals between deployments of similar length of time but different starting dates, than between assemblages of different age, as shown by the number of syllids (Fig. 6A). These worms increased in abundance as AUHs were deployed for longer, with similar patterns in each site.

The patterns of abundances of most taxa, however, gave variable results between sites and times of deployment, as illustrated for the abundance of nereidids in Fig. 6B. Neither length of period of deployment, nor particular times of deployment, showed consistent patterns of colonization across sites.

A few taxa showed apparent "seasonal" trends similarly across sites. Therefore, the gastropods, *Amphithalamus incidata* (Fig. 6C) and *Rissoella micra* (Fig. 6D), showed increased colonization at times 5 and 7 (in each site). This led to very much greater abundances in the second 2-month period (T6) than the first (T2). The AUHs that had been left for four months, in contrast, showed very large differences between sites.

In general, however, no consistent patterns could be found among taxa, which suggests that the change through time of the entire assemblage was not mostly associated with predictable changes in abundances of particular taxa or sets of taxa.

4. Discussion

The results demonstrate that successional processes occur in the establishment of the assemblages. There is progressive change that is "directional" (Platt and Connell, 2003). Assemblages seem to converge within a few months from different starting scenarios. There was, in fact, greater change from 2 to 4 months than from 1 to 2, but this was not simply due to temporal changes in the availability of taxa to colonize. If that were the explanation, there should have been greater agreement between natural assemblages and those constructed by averaging assemblages which developed over shorter periods. This study did not demonstrate the "completion" or climax of succession, which would have required longer periods with no major, further change. The period of 4 months used here is consistent with the recommendations by Gee and Warwick (1996) and Rule and Smith's (2005) findings that colonization and development of assemblages would be complete by about 5 months. In the pilot experiment, the scourers deployed for 6 months that were not destroyed by bad weather had assemblages similar to those after 3 months. This implies that succession stabilises somewhere between 3 and 6 months. So, a period of 4 months should be considered adequate. To know for sure requires replicated investigation of larger periods of deployment. Whatever the final outcome, it is clear that deployment for longer than 1 or 2 months is necessary for reliable sampling.

It is, however, interesting to note that Myers and Southgate (1980) recorded only 15 species of gastropods after a single one month period of deployment of pot-scourers in a rocky intertidal area. In the present experiment, there was a total of 53 species of gastropods after one month of deployment (reflecting subtidal rather than intertidal habitats, different season of the year, different bioregion, etc., from Myers and Southgate's (1980) study). The total number of species did not change much from 1 to 4 months of deployment, but the pool of species being sampled was greater for 1-month than for 4-month deployments (see above). The number of taxa of polychaetes increased from 10.8 in 1-month deployments to 17 after four months of deployment (an increase of 58%). This makes it difficult to determine what is the optimal period of deployment of AUHs where the objective of the study is to sample the biodiversity of a region, as in Gee and Warwick (1996). If the period that generates the greatest number of species varies from one bioregion to another, global comparisons of biodiversity are compromised if data came from the same period of sampling in all regions.

Assemblages did not develop by increasing the number of taxa through time. Replacements of taxa occurred. This process differs between polychaetes and gastropods, so it is not an inevitability of passage of time. Also, taxa tended to be distributed across replicates in similar ways whatever the time or period of colonization, so they were not becoming more frequent in replicated assemblages through time. Seasonal (i.e. starting 2 months apart) differences were quite small compared with differences in development of assemblages starting one month apart.

Notably, however, there was extraordinarily close agreement in the development of assemblages in 2 sites 100 m apart. This was surprising, given the usually encountered spatial variability in similar assemblages sampled at such distances apart (Morrisey et al., 1992a; Chapman, 1998; Kelaher, 2005). This finding was

consistent with the study by Rule and Smith (2005), who found little variation at a scale of 100 s of m in assemblages developing in pot-scourers. They did not provide any data about dissimilarities of assemblages, so it is impossible to compare the present results with theirs. The data they presented for univariate analyses were confusing because some of the variance components they presented for 100 s of metres distance would, in fact, have been incalculable (negative). There was, however, as here, no evidence for differences at the spatial scale of 100 m. This implies that much of the natural variability encountered is related to the previous history of patches of habitat prior to colonization, which did not vary in this experiment and that of Rule and Smith (2005). This result of decreased small-scale variation in AUHs compared with natural pieces of habitat is not universal. For example, fouling assemblages developing on artificial surfaces (panels) show very large small-scale temporal and spatial variability (Keough, 1983), despite having identical shape, size and history.

Numerous pathways, patterns and processes are known for succession of different types of assemblages (see the reviews by Huston and Smith, 1987; Whitlatch et al., 1998; Hall et al., 2000; Platt and Connell, 2003). In some assemblages, there are fairly predictable starting conditions, e.g. the early colonization of cleared patches of rocky shore by diatoms and then filamentous algae. What then happens can lead to one of several possible outcomes, depending on the influences of competitors and predators (Connell, 1975), disturbances and prevailing environmental conditions (Dayton, 1971; Connell, 1975) or variation in supply-side ecology — i.e. processes of recruitment (Underwood and Denley, 1984). Usually, the possible end-points or climaxes are limited in number (Sousa, 1979a,b; Underwood et al., 1983; McCook and Chapman, 1991, 1993). Thus, one initial set of conditions can lead to one of only a few structures of an assemblage.

Then there are assemblages that can start with various structures and proceed along different pathways until, eventually and predictably, some dominant user of resources arrives and competitively eliminates numerous (most) other components of the assemblage. In this scenario, there can be several possible developments, but one climax. This is, for example, what has been described where mussels recruit and survive in sufficient numbers to outcompete all other space-users on a rocky shore (Paine, 1974, 1980). Whatever variable structure of assemblages was developing, the climax is a monoculture of mussels on the primary substratum. Of course, the assemblage as a whole, including animals on and amongst the mussels is more complex (Lohse, 1993), but there is supposedly only one user of primary space.

Unlike Platt and Connell (2003) and as done by Gleason (1926, 1927), succession as used here includes changes in relative abundances of species. Because changes in the structure of entire assemblages are an important component of temporal and spatial variation, all forms of change need to be considered before variation will be understood. Most models of succession (e.g. Connell and Slatyer, 1977; Tilman, 1990; Platt and Connell, 2003) still do not include the variance in which taxa arrive first and the supply-side issues associated with this (Sutherland, 1980; Underwood and Denley, 1984). There is an assumption that categorising species as early or late successional colonists is more important. It is not obvious why this consequence of life-history should be more important than others — such as the capacity to tolerate a wide range of co-existing species.

The present results allow falsification of some mechanisms of succession. The process operating is not rigid, deterministic or Clementsian succession (Clements, 1916). There was no suggestion here that early development of assemblages (after one month) always had the same structure. There were major differences among 1-month deployments. It is always possible that the very earliest events (i.e. in shorter periods than one month) were similar, but, if so, there must have been divergence before assemblages were sampled at one month.

There may have been variation in what starts a process of succession, but determinism in the outcomes of processes occurring later. This raises some dilemmas in designs of experiments to distinguish amongst processes. For example, there may be indeterminism in the starting sequences of arrivals and interactions, followed by successional processes leading to one climactic assemblage (i.e. the end-point is predictable). Alternatively, there may be similar uncertainty at the start of a succession, but different end-points can result (Sutherland and Karlson, 1977). In some cases, the different end-points may be entirely predictable from the initial stages (see Underwood et al. (1983) for an example involving algae, barnacles and limpets). Thus, each "start" leads to a predictable "end"; different starts lead to different ends (e.g. Connell, 1975). Alternatively, there could be different starting colonization, followed by one of a small number of processes, each of which can lead to one of a set of outcomes.

To differentiate between these requires repeated experimentation to determine the final outcome(s). In one temporal sequence (as described here), it is not

possible to know that the end-point is a consistent, predictable one, or that it is one of only a few possible end-points or is, in fact, one of numerous possibilities. Most studies of succession in complex assemblages have limited temporal replication to determine the consistency of end-points. In order to understand the processes responsible for the patterns described here, more examples of studies investigating variations in time (and space) are needed.

Further, the life-histories (including timing of reproduction, mode of dispersion, etc.) of most of the taxa found in experimental assemblages are not known or are only patchily known for some regions where they are found. Analysis of functional groups of, say, consumers (e.g. Gwyther and Fairweather, 2002) may prove fruitful, but preliminary analysis of the gastropods (for which, at least, some natural history is understood; Beesley et al., 1998) is not very promising (unpub. data). Knowing that differences in characteristics of life-history make a major contribution to processes of succession (Sutherland and Karlson, 1977; Sousa, 1979a,b) does not help if, as here, there are hundreds of species involved and their life-histories are uncertain.

Developing a synthesis of the nature of succession in complex, diverse assemblages and processes leading to definable end-points of structure of these assemblages requires more examples of the time-courses and influences of season on the outcome.

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