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DEVELOPMENT AND LONG TERM DYNAMICS OF A FOULING ASSEMBLAGE OF SESSILE MARINE INVERTEBRATES

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The construction of a new pier in upper Spencer Gulf, South Australia, was used as an opportunity to test theories about recruitment and dynamics of subtidal assemblages of sessile invertebrates. The fouling fauna was monitored for *ca* six years after initial immersion of piles using photographs of fixed positions and direct observation by divers. Assemblages were traced through time using non-metric multidimensional scaling (MDS). Faunal composition differed at sites along the pier throughout the study, but the composition at all sites tended to change in a similar way over time, and seemed to be changing more slowly near the end of the study. Abundances of key taxa fluctuated markedly from site to site along the pier, but for some taxa a trend was discernible over and above the variability. Predictions based on experiments on piers in more sheltered waters in an adjacent gulf were not fulfilled; although over 50% of pile surface area was covered by encrusting or mound-forming colonial animals such as sponges and colonial ascidians, solitary organisms such as bivalves and solitary ascidians which were expected to be overgrown persisted in great abundance throughout the study. Significant differences amongst sites after *ca* six years, both in assemblages and in abundances of key taxa, did not match environmental variables such as degree of shading, depth of seabed, disturbance due to wave action, or release of treated ballast water, although there were signs of an effect of high current speeds associated with a local gyre.

KEYWORDS: ANOSIM, assemblage, community, fouling fauna, modular animals, recruitment

INTRODUCTION

Fouling assemblages on large artificial substrata have been studied not only as a practical problem but also as experimentally convenient mimics of natural substrata in the same area (Kay & Keough, 1981; Kay & Butler, 1983; Keough, 1984a; Butler, 1986, 1991) and it has been possible to propose and test models for the ecology of the organisms. Sessile organisms in Gulf St Vincent, South Australia occupy variously sized patches ranging from small, such as the shells of the bivalve *Pinna bicolor* Gmelin, to large, such as piers and large rocky reefs (Butler & Keough, 1981; Keough, 1983, 1984a,b; Kay & Keough, 1981; Kay & Butler, 1983). Small patches bear a community quantitatively different from that of large patches. Kay and Keough (1981) proposed that small patches serve as refuges for poor competitors for space, because there is a low probability of a dominant competitor recruiting to the patch. Aspects of this hypothesis were examined experimentally in Gulf St Vincent by Butler (1986, 1991), but the present paper reports an opportunity to test the conceptual model in a different location and on a new structure.

In early 1982, SANTOS Ltd began construction of a hydrocarbon-loading facility, to be named Port Bonython, at Stony Point in Spencer Gulf, South Australia. It included a

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steel pier running 2.4 km from shore, to reach the 20 m depth contour. The facility was designed to receive liquid hydrocarbons by pipeline from the Cooper Basin 659 km inland to the north and, after fractionation ashore, to load crude oil, condensate, ethane, propane and butane onto tankers. There was concern to monitor the possible environmental effects of this operation, because northern Spencer Gulf is considered environmentally sensitive, being a relatively enclosed water body of high conservation value and supporting important fisheries. This study was designed as part of that monitoring.

The programme, however, also gave an opportunity to observe the development and dynamics of the fouling assemblage on a newly-created structure over a period of more than five years in an area of strong tidal currents, generally moderate wave exposure, and large seasonal fluctuations of temperature and salinity. This paper concerns the dynamics of the assemblage.

This is not the place for a discussion of the idea of community (see *e.g.* Begon *et al.*, 1990; Underwood, 1986), except to note that no initial assumption is intended here as to whether a suite of coadapted and stably coexisting species is being studied. In this paper the term "assemblage" is used to mean the organisms living together on the pier, without further connotations. Whether there are predictable co-occurrences, coadaptations, important interactions, *etc.* between species are subsequent questions.

Knowledge of the dynamics of fouling assemblages in SA waters (Kay & Keough, 1981; Kay & Butler, 1983; Keough, 1984a; Butler, 1986, 1991; Butler & Chesson, 1990) had indicated a substantial dependence on the long life and vegetative growth of modular organisms in maintaining the composition of the assemblage and a significant contribution from locally-produced, short-lived pelagic larvae (Davis & Butler, 1989) so that the assemblage was largely "self-seeding" in two respects. Such systems do not appear to be dominated by species with teleplanic larvae (Butler & Keough, 1990). This work had, however, all been done on structures built a long time earlier and bearing large, apparently stable populations of sessile organisms, some of great age. The construction of the pier at Port Bonython made a large amount of bare space available for colonization in an area where the seafloor is predominantly sandy and available hard substrata are small (low-profile reefs, isolated small rocks, *P. bicolor* shells) but commonly have well-developed epifaunal assemblages (Shepherd & Sprigg, 1976; Shepherd, 1983). Larvae colonizing the pier would probably arise from sessile organisms on these nearby small substrata, on larger, but low-profile rocky reefs to the east and west of the pier, or on large artificial substrata further away (the nearest being the port of Whyalla, 16 km to the west). At the very least, early colonization of the pier would give an indication of the species-composition and density of pelagic larvae available in this Gulf. However, the greatest interest was in the dynamics of the fauna on this large structure after its initial colonization. Although the authors had worked in various degrees of wave action, they had little knowledge of assemblage dynamics in an area of such strong tidal currents as occur at Port Bonython. Would the assemblage become "stable" and largely "self-seeding" like the sites already studied?

The conceptual model developed at other sites led to the following predictions about the new pier:

i. the initial colonization by pelagic larvae would reflect the relative abundance of potential parents on the surrounding small substrata, and would also reflect the relative numbers of pelagic larvae produced by these species. Thus, initial composition would be biased towards the better-dispersing, but shorter-lived and competitively inferior organisms predominant on small patches, notably spirorbid and serpulid polychaetes, barnacles, bryozoans and certain bivalves.

ii. there would then be succession towards an assemblage dominated by long-lived, competitively superior modular organisms such as sponges, certain cnidarians, colonial ascidians and certain bryozoans. Once they had become established, it was predicted that these forms would increase by vegetative reproduction. Thus, notwithstanding the continued arrival of dispersive larvae from elsewhere, colonisation of any newly-created vacant space would largely reflect the composition of the pier assemblage; the assemblage would become stable and to a large extent self-seeding.

For logistic reasons, recruitment could not be measured in this study using the techniques of Keough (1983) and Butler (1986), and therefore the primary prediction to be tested was that of a succession to a stable community dominated by modular organisms.

The specific aims, therefore, were:

1. to test the hypotheses that
   i. the fauna on different groups of pilings would converge to some common composition dominated by modular organisms (even though the piles were not installed simultaneously)
   ii. the assemblage would converge to a "stable" condition (showing little change with time; *cf* Kay & Butler, 1983; Keough & Butler, 1983)
2. if the fauna on different groups of pilings did not reach a common composition, then the question would be asked which species contribute to similarities and differences between groups of piles, and hypotheses would be formulated about the possible effects of environmental variables.

MATERIALS AND METHODS

Study Site

The location of Port Bonython (33°1'S, 137°46'E) is shown in Figure 1. The pier runs in a southerly direction away from the shore and consists of a relatively narrow trestle bearing a roadway and pipe racks 11.5 m above sealevel, running out to a substantial loading platform (50 m × 25 m). The pier is supported by cylindrical steel piles, generally 1016 mm in diameter. The piles of the trestle stand in small groups called "bents", 24 m apart; most bents consist of two sloping piles at right angles to the axis of the pier but at intervals there are "anchor bents" of four sloping piles, two of them in line with the axis of the pier and two perpendicular to it. Observations were made on the north-south piles (in line with the axis of the pier) in anchor bents. Although the loading platform is largely supported on vertical piles it, too, has some north-south sloping anchor piles, and observations were made on these.

Construction of the pier began with the loading platform (LP) early in 1982; the trestle was then constructed from shore. The piles of bent 5, the first offshore, were driven in the week ending 10 July 1982 and the bents used in this study were driven between 6 November 1982 and 21 April 1983. They were bents 45, 66, 76, 86, here referred to as bents 1, 2, 3 and 4. Fixed quadrats were installed on 15 February 1983 (Bent 1 and LP), 9 April 1983 (Bents 2 & 3) and 20 June 1983 (Bent 4). Thus, observation of the colonization of the pier began before construction was completed and most of the fixed sites have been monitored from a very short time after the piles were driven for a period of 5.5 years.

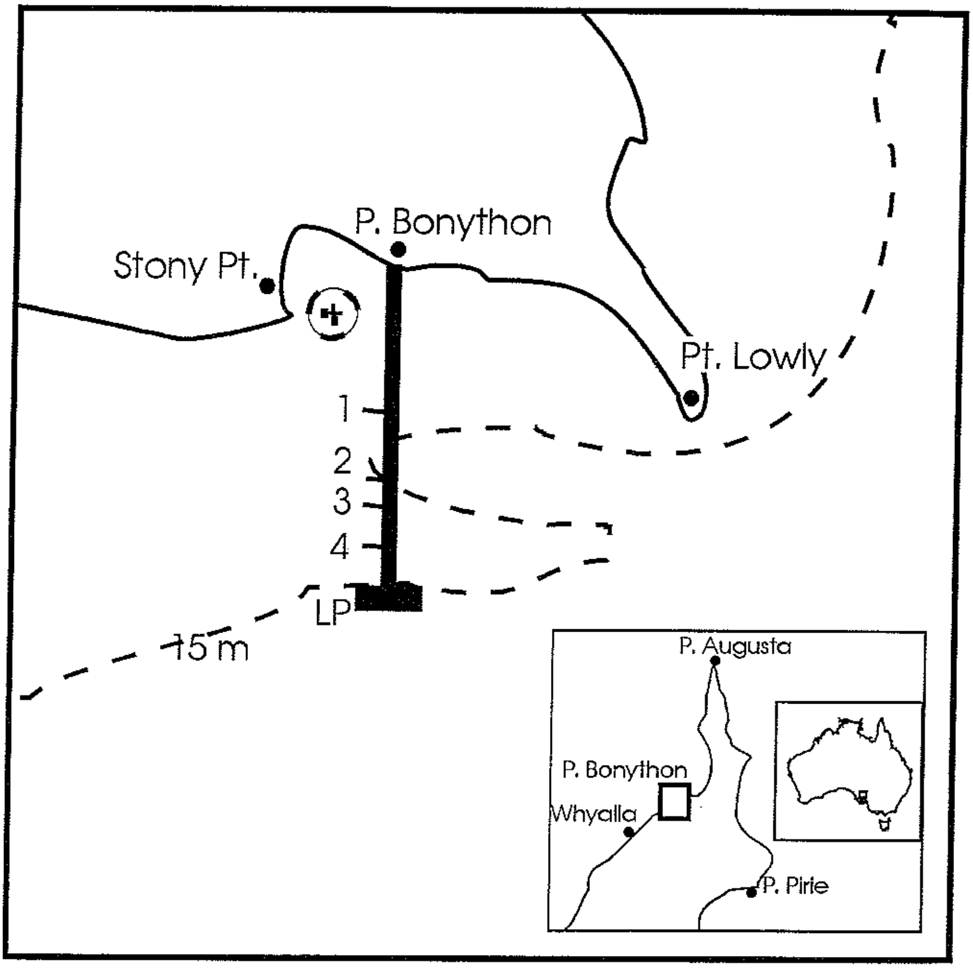


Fig. 1 The SANTOS Ltd pier at Port Bonython. Positions of bents used for monitoring are indicated as 1–4 and LP. (+) = the rocky reef sampled west of the pier. ---- = the 15 m depth contour. Inset: location of Port Bonython in Spencer Gulf, South Australia and location of Spencer Gulf in Australia.

In order to monitor the development of the fouling assemblage starting with bare (coal tar epoxy coated) piling surfaces, permanent quadrats were established on two piles at each of the four trestle bents plus the loading platform. Four quadrats were set on each pile, with their top edges at depths of about 5 m, 5.8 m, 6.6 m and 7.4 m below low water level. Beginning at the top of each pile, alternate quadrats were on the north, south, north, south side of the pile. The top left-hand corner of each quadrat was marked with a knot in a rope tied around the pile; the rest of its extent (0.3 m × 0.56 m) was outlined by the camera frame when photographed.

Each quadrat was photographed on 35 mm Ektachrome 64 ASA colour slide film using a Nikonos III camera and electronic flash. A procedure of qualitative monitoring was also used, in which divers swam up and down the full length of piles, writing on a pre-ruled slate estimated rankings for the abundance of certain species or broader animal groups, and noting any other features of particular interest. This was done on all piles on which fixed quadrats were established, on the date of their establishment and on each subsequent visit, and also on other piles from time to time. The rocky reefs off Stony Point itself and off Point Lowly (Fig. 1) were inspected on two occasions, *viz.* 22 June 1983 and 16 July 1986.

On 24 January 1986 the quadrats were re-marked or, where the old marks had completely disappeared, replaced in about the same positions. The quadrats were photographed and notes made on the fauna in the normal way after marking. Thus, a partially new series of fixed quadrats begins from that date.

Visits were made on 17 dates. Data from the following dates (with arbitrary identifying numbers) are reported in this paper.

Date	Date number	
10 July 1984	1	
29 May 1985	2	
24 January 1986	3	(quadrats re-marked)
15 July 1986	4	
5 February 1987	5	
29 June 1987	6	
13 January 1988	7	
8 June 1988	8	
12 January 1989	9	

On date 9, divers counted, *in situ* underwater in the photographed fixed quadrats, a number of species routinely counted from slides, as well as taking photos both of those fixed quadrats and of a set of randomly-positioned quadrats. This enabled a check on the error in counting unitary (solitary) species from slides and a check on the representativeness of the fixed quadrats. Divers also made *in situ* estimates of cleared space; this included bare space, which was routinely estimated from slides, but also space recently cleared even if now reoccupied by a new, encrusting layer; this served as an index of disturbance (probably mainly due to wave action) in the assemblage.

Identification of Flora and Fauna

Representative specimens were collected by divers whenever they found what appeared to be a new species, and preserved on shore the same day. Some have been identified by museum specialists, some in the laboratory using the keys in Hale (1927–1929), Kott (1985, 1990, 1992) and Shepherd and Thomas (1982, 1989), but many cannot be identified to species and, in any case, cannot be reliably distinguished in photos or in the field. Therefore, some grouped categories are used. There is evidence that identification to taxonomic levels as high as family and even phylum can lead to the detection of environmental patterns (Warwick 1988, Warwick & Clarke 1993) and this approach has been used in earlier work (Butler 1986, 1991).

Interpretation of Photographs

The interpretation of photographs of fixed quadrats was more difficult than at other sites at which this technique has been used (*e.g.* Kay & Butler, 1983), because of the preponderance of arborescent forms growing on the pilings. It was expected to become more effective as more encrusting forms became dominant but, although there was a period after the dominance of hydroids when photos were easily interpreted, arborescent modular organisms, especially the soft coral *Telesto multiflora* Laackmann, later became so abundant that photos became increasingly difficult to read.

Percentage cover was estimated from the slides using a grid of regularly spaced dots and counting the number, hence percentage, of dots intersecting a given species. There are difficulties with this method (Foster *et al.*, 1991; Dethier *et al.*, 1993) but it was the best method available with extremely limited underwater time.

Of the species or groups that could be distinguished in the slides (Table 2), some were too sporadic in occurrence for statistical analysis. Twenty-six species or groups were included in multivariate analyses (ten that could be consistently identified and counted as individuals and 16 that could be estimated as percentage cover; bare space was a 17th variable scored as percentage cover). Of these, seven were sufficiently abundant for univariate analysis (three counted as individuals, and three species plus bare space scored as percentage cover). Table 2 indicates which species/groups were used in each type of analysis.

Analysis of Data

This is a nested design in which position along the pier (bent) is a fixed factor (5 levels), piles within bents a fixed, nested factor (2 levels), and quadrats within piles are considered as four random replicates. Depth and aspect are partially confounded, and the positioning of quadrats at four depths and two sides on the pile is viewed as merely a way of interspersing them; determination of absolute depth during installation was inaccurate.

The design was a compromise; because the quadrats are fixed in position, readings taken at different dates are not independent and so "time" strictly cannot be examined as a factor. Fixed quadrats, however, were required in order to observe succession and to observe the life-cycles of individually recognizable animals. Lundalv (1985) has argued in favour of fixed photographic quadrats, but there is no strict argument that will overcome the non-independence of successive observations on fixed sites. Comparison between bents at one time is valid; the non-randomness of the lowest level of variation is unlikely to seriously influence any conclusions about differences between bents. A set of random quadrats was photographed on date 9 as a partial check on this.

Temporal changes in the fauna were analysed by a) using multivariate methods to examine the similarity between bents and how that similarity changed with time; b) plotting the abundance of particular taxa against time.

Considered at date 9 only, the statistical significance of univariate differences between bents and between piles within bents was tested by analysis of variance for those few variables that met the assumptions (after log(x+1) transformation). Significance tests of multivariate differences between bents and between piles were made using the "ANOSIM" (Analysis of Similarities) of Clarke (1993).

ANOSIM is a non-parametric analogue to a multivariate analysis of variance (MANOVA) without the assumption of multivariate normality. ANOSIM has an additional advantage over MANOVA in being able to detect differences between groups without the need for assumptions of constant spread within each group (Clarke, 1993). ANOSIM compares ranked similarities between and within groups selected a priori using a randomisation test for significance. A nested ANOSIM was used to test effects of piles and bents at date 9. All ANOSIM tests involved 1000 simulations using the PRIMER package (versions 3.1 and 4.0) from Plymouth Marine Laboratory, UK (Clarke & Warwick, 1994).

Non-metric multidimensional scaling (MDS) is an ordination technique that uses the same matrix of ranked similarities as ANOSIM; it displays samples in low (usually two) dimensional space while retaining as nearly as possible the similarity rankings between samples. The degree to which rankings are not preserved in the two-dimensional plot is indicated by a stress value. Analysis of the similarity matrix used in MDS and ANOSIM has also been used to highlight the species making the largest contribution to between-group differences (Clarke, 1993).

For these multivariate analyses, raw counts were transformed using $x^{0.25}$ to emphasise the distribution of less common species in the analysis. The Bray-Curtis similarity coefficient was used throughout, as a meaningful and robust measure (Clarke, 1993). Counts and percentage cover were used together in these analyses. The difference in scale could, theoretically, have had a large influence on plots. MDS analyses were also done using standardised data, but patterns were very similar to those without standardisation, and are not shown.

Before doing the main analysis, the following four checks were made of the validity of assumptions.

1) Comparison of random and fixed quadrats photographed on date 9, to confirm that the fixed quadrats are "representative" of the pier. This cannot remove the problem of non-independence between dates but can confirm that the systematic placement, used for interspersion, has not introduced some bias. The eight quadrats from each bent (2 piles) were considered as replicates, so that there were 8 replicate fixed quadrats and 8 replicate random ones per bent; thus there is an orthogonal design with two factors, bent (5 levels) and fixed *vs* random quadrat (2 levels). A MANOVA on log-transformed data for species common enough to use parametric methods (and using Pillai's trace, V, as recommended by Johnson & Field, 1993) showed no difference between fixed and random quadrats nor a significant interaction with bent (Bent: $P < 0.001$; Fixed *vs* Random: $P = 0.173$; Interaction: $P = 0.481$).

2) Comparison of counts from photos of fixed quadrats with direct counts by divers on date 9, to confirm that photo reading is, at least, consistent even if biased. The comparison was done using paired t-tests and confirmed that although counting of unitary organisms from photos underestimates numbers of some species (*Malleus meridianus* Cotton, *P. bicolor, Herdmania momus* (Savigny), less so for *Phallusia obesa* (Herdman)) there is no consistent bent effect across species (Table 1).

Table 1 Results of paired t-test comparisons of counts from photos with direct counts by divers on date 9. Values are probabilities of test statistic under the null hypothesis. For individual bents, n = 8 pairs, for all bents, n = 40 pairs. Direct counts were greater than counts from photos, whether significant or not, except where marked by (–).

Bent Species	1	2	3	4	5	All bents together
M. meridianus	0.001	0.031	0.269	0.001	0.510	<0.001
Polycarpa spp.	0.090	0.111	0.919(–)	0.460	0.837(–)	0.126
P. obesa	0.104	0.435	0.170	0.200	0.365(–)	0.043
P. bicolor	0.351	0.351	0.039	0.351	0.363	0.018
H. momus	0.026	0.262	0.014	0.670	0.004	<0.001

3) Correlation of differences between photo and direct underwater counts with cover of the soft coral *T. multiflora* to check whether a bias develops as cover of *T. multiflora* increases towards the end of the study, obscuring other species in the

photographs. The differences between field and photo counts were not correlated with cover of *T. multiflora* (*e.g.* Spearman ρ values were: *M. meridianus* 0.19, *Polycarpa* spp. 0.28^*, *P. obesa* 0.10, *P. bicolor* –0.27, *H. momus* –0.12; *P* slightly less than 0.05 only for *Polycarpa* spp.), indicating that at dates earlier than 9 a similar result would have been obtained. Thus, although the data from photographs cannot be used as absolute estimates of abundance, they are proportional to abundance, and adequate for comparison between bents and times.

4) Comparison of N-facing with S-facing quadrats to confirm that these did not differ significantly and could be treated as simple replicates within a bent. This was done by simple 2-factor analyses of variance on log (x + 1) transformed data for *T. multiflora* (the species most likely to make a difference to the conclusions because of its effect in obscuring other species), *M. meridianus, Botrylloides* spp., *P. obesa, Polycarpa* spp. and *H. momus* on date 9. There were no significant effects of direction nor of interaction between direction and bent. It was concluded that quadrats could be treated as simple replicates.

RESULTS

Species Recorded

At least 61 species have been distinguished on the pilings. Not all have been identified and the number is almost certainly higher. The species identified, and the groupings of species used in analysis, are listed in Table 2.

Early Development of the Fauna on the Piles

Photos were not reliably readable (because of extensive cover of arborescent hydroids) until two years after construction began, and this paper is not concerned with early succession on the piles. However, the sequence from divers' notes and qualitative examination of the photos are outlined here .

Table 2 Organisms collected from the piles of Port Bonython Pier, February 1983 to July 1986 and categories recognized in scoring slides. The abundance of those marked * was used in certain multivariate analyses and of those marked ** also used in univariate tests for differences between bents and changes through time. N = number per quadrat counted; %C = percent cover estimated.

Higher Taxon		sp/group	type of scoring
Porifera		*Callyspongia* sp.	*%C
		Dendrilla rosea Lendenfeld	%C
		unidentified "Honeycomb sponge"	*%C
		Sycon sp. and several other spp. of pale coloured sponges, scored together as "White Sponge"	**%C
		12 to 16 other unidentified spp. of sponges	
		Other Sponges, scored together	*%C
Cnidaria	Hydrozoa	*Halocordyle disticha* Goldfuss	**%C
		Tubularia ralphi Bale	
	Anthozoa	*Telesto multiflora* Laackmann	**%C
		unidentified anemone	

Ectoprocta		*Triphyllozoon* sp.	*%C
		Bugula neritina (Linnaeus)	
		Lancepora obliqua (MacGillivray)	
		Celleporaria sp.	
		Petralia undata MacGillivray	
		+4 unidentified spp	
		Bryozoans other than *Triphyllozoon* sp. were analysed as "all other bryozoans"	*%C
Mollusca	Bivalvia	*Mytilus edulis planulatus* Lamarck	
		Modiolus areolatus Gould	
		Mussels scored together as	*N
		Ostrea angasi Sowerby	
		Hiatella australis (Lamarck)	
		Malleus meridianus Cotton	**N
		Electroma georgiana (Quoy & Gaimard)	
		Anomia trigonopsis Hutton	
		Chlamys asperrima (Lamarck)	
		Chlamys bifrons (Lamarck)	
		Two species of *Chlamys* scored together as	*N
		Pinna bicolor Gmelin	**N
Mollusca	Gastropoda	unidentified limpets	
		unidentified neogastropods	
Annelida	Polychaeta	*Galeolaria* sp.	
		at least 1 unidentified serpulid	
		Galeolaria & unidentified serpulids analysed together	*N
		unidentified terebellids	
Arthropoda	Crustacea	*Balanus amphitrite* Darwin	
		Elminius sp.	
		barnacles together analysed as	*N
		Leptomithrax australiensis (Miers)	
		Cryptodromia octodentata (Haswell) + at least one sp.	
		unidentified small crab	
Chordata	Ascidiacea		
	solitary ascidians	*Polycarpa pedunculata* Heller	
		Polycarpa papillata (Sluiter)	
		Polycarpa spp., mostly *P. pedunculata*, scored together	**N
		Herdmania momus (Savigny)	*N
		Phallusia obesa (Herdman)	*N
		unidentified at least 5 more species scored together	*%C
	colonial ascidians	*Botrylloides leachii* (Savigny)	
		B. leachii together with one or more unidentified botryllid species*	%C
		Botrylloides magnicoecum Hartmeyer	
		Didemnum sp.	*%C
		Trididemnum sp.	
		Clavelina moluccensis (Sluiter)	
		Relatively uncommon + unidentified colonial species, including *C. moluccensis*, scored together	*%C
Algae		Foliose red algae	*%C
		Corallines	*%C
		Green algae	*%C
Remaining variables analysed:		Bare piling space	**%C
		Unidentifiable colonies	*%C

Many bivalves, especially *Electroma georgiana* (Quoy & Gaimard), *M. meridianus*, *Ostrea angasi* Sowerby and *Anomia trigonopsis* Hutton, were present early, with much bare space. Hydroids were very abundant early. Percentage cover increased rapidly after four months, and was near 100% after six months. Encrusting modular organisms occupied an estimated 30% of space after six months. After a little more than eight months, sheet-, mound- and tree-form modular organisms, especially sponges and *T. multiflora*, were abundant along with unitary organisms, especially bivalves and ascidians. Little difference can be discerned in the pattern of colonisation between bents, despite the different dates of their establishment. Exceptions are the date of initial arrival of *T. multiflora* and perhaps of *M. meridianus* both suggesting a limited period of dispersive recruitment in late summer, and a bloom of unidentified pink and grey mound-forming sponges which were very abundant on the older piles at the LP and bent 1 at a time when bents 2, 3 and 4 were only two to four months old; these then died off from the LP and bent 1 and never became established on the newer bents.

Dynamics of the Assemblage as a Multivariate Process

The 27 variables marked * and ** in Table 2 were included in multivariate analyses both to examine the changes in the assemblage on the five bents through time and to compare them at one time. Results are presented for dates 2, 5 and 9, after a little less than two, four and six years respectively, *i.e.* three, five and seven years after the driving of the first piles of the LP. These dates were chosen because they were spaced approximately two years apart and each was in the warmer months of the year when the data were not distorted by winter-blooming colonial ascidians; the winter patterns, dates 1, 4 and 8, are very similar.

Analyses were done at two levels of resolution: individual quadrats (there are 40 of these on any one date, so the display becomes very confusing for more than one date), and means over the quadrats for each bent (hence, five per date, 15 over three dates). The conclusions were almost identical whether individual quadrats were plotted (and then the centroid for each bent estimated by eye — this plot is not shown) or means were plotted for bents.

Figure 2 shows the MDS plot for averages over the eight quadrats within each bent, at dates 2, 5, 9. Broadly, the bents move across the plot, very roughly in parallel. The bents seem as similar at date 2 as at date 9 though it is important not to take too literally the appearance of the points on a two-dimensional plot. Although bents appear to differ on date 2, the differences are not explicable by their dates of construction and subsequently, though clearly still changing, they changed in similar ways. The same conclusion is reached on examining data from the "winter" dates 1, 4, and 8. These MDS results accord with the qualitative observations during diving, that there was rapid convergence, within 15 months or more, to a condition that looked much like the LP had when first seen, when it was aged a little over a year.

The LP, standing alone, had developed a rich fauna with over 50% cover of modular, encrusting and mound-form organisms although unitary organisms (bivalves and ascidians) remained abundant, as they would for the next six years. This indicates effective colonization and rapid growth, in a high-current area with seasonally high temperatures.

It might be thought that the multivariate results would be dominated by abundant species that were already present (if not yet abundant) early, and that the bents moved "in parallel" as those species altered in abundance, *i.e.* that the method might be insensitive to relatively rare species entering late in the successional sequence. However, the analysis was done on 4th-root transformed abundances, thus emphasising rare species. Further, the analysis for date 9 (below) was repeated using only presence/absence, not abundance, of species or groups, with almost the same result as on abundances.

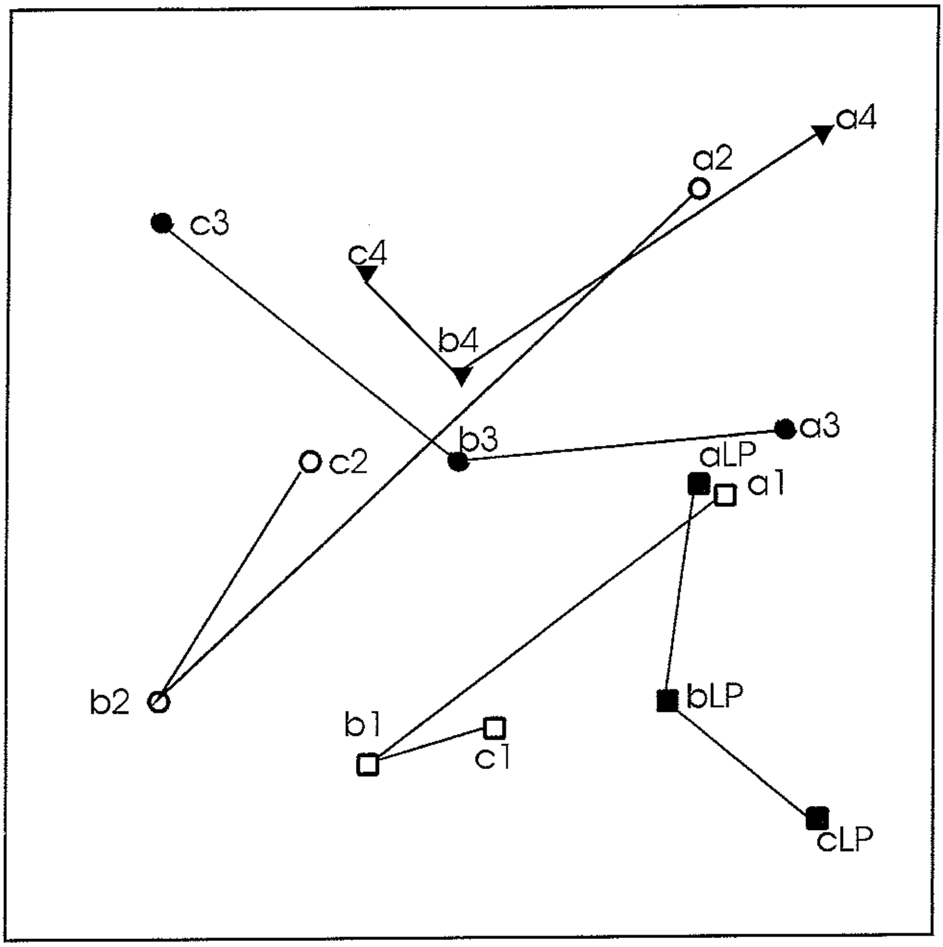


Fig. 2 Nonmetric multidimensional scaling plot in two dimensions of the similarity (Bray-Curtis) between bents (8 quadrats within a bent averaged) at three dates. Dates are represented as a = date 2, b = date 5, c = date 9 and bents by 1, 2, 3, 4, LP. Stress = 0.14

The MDS plots are not very good fits; in all the analyses conducted, the stress values were acceptable (Clarke, 1993) but not low. There is much variation within bents and not very clear differences between bents, but the ANOSIM results do suggest that the differences indicated in the MDS plots are significant.

Differences between Bents after ca. Six Years as a Multivariate Process

Although there is considerable overlap amongst bents in the MDS for Date 9 (Fig. 3), 5.75–7 years after immersion for different groups of piles, the differences between bents are significant (One way ANOSIM using 8 quadrats as replicates for each bent, $P < 0.001$, nested ANOSIM, piles ns ($P = 0.07$), bents $P < 0.05$). In pairwise comparisons, bent 1 is different from all others, as is the LP, and bents 3 and 4 differ significantly. If a strict α level of 0.005 (simple Bonferroni adjustment for multiple tests) is used then only pairs 1,3 and 3, LP differ significantly. The analysis of the contributions of different groups to the similarity shows that there is no simple or global explanation for differences between bents but *Halocordyle disticha* Goldfuss, *T. multiflora*, *Polycarpa* spp. and White Sponge are major contributors with *M. meridianus* and other sponges occasionally important. The MDS for date 9 using presence/absence only, rather than abundances, is very similar to that in Figure 3 (ANOSIM, $P < 0.001$; nested ANOSIM, piles ns ($P = 0.27$) bents ns ($P = 0.064$)). Significant pairwise differences at the uncorrected 5% level are (1,3), (1, LP), (2, LP), (3, LP). Bonferroni adjustment for multiple tests would set the critical point at 0.005; no pairs fell below this, but 1,3 and 3,LP scored $P = 0.01$, well below any other pairs.

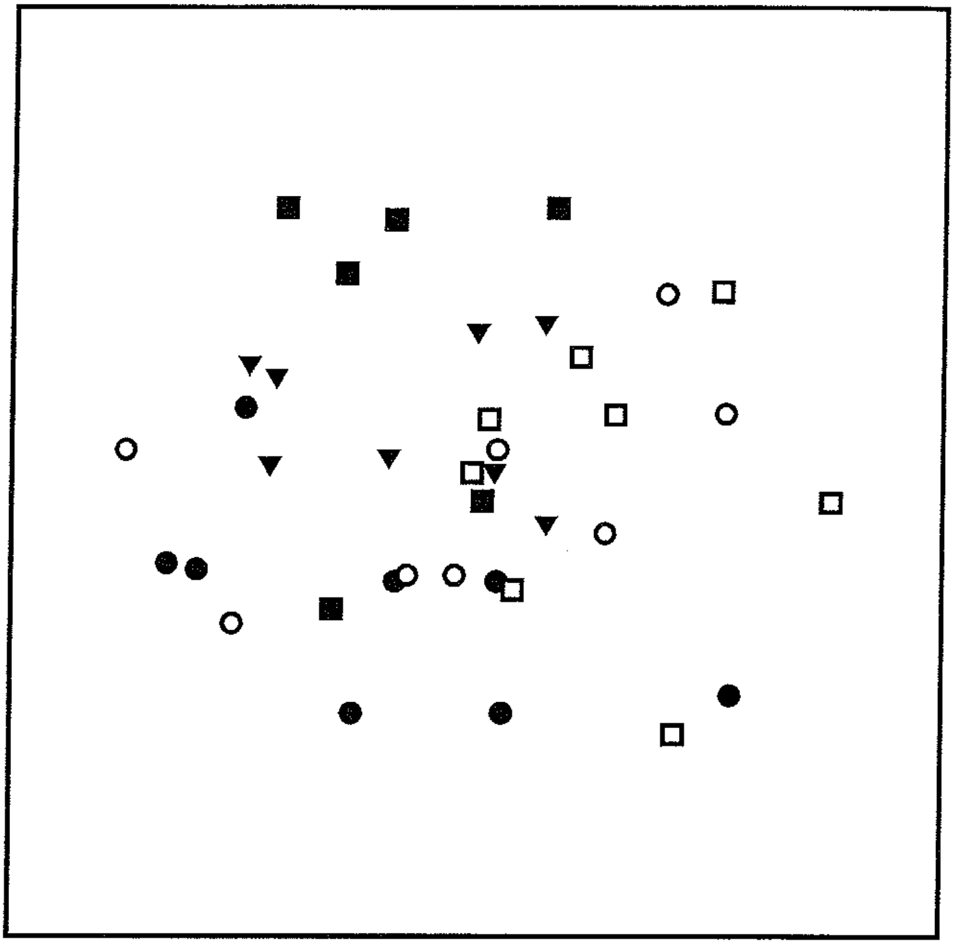


Fig. 3 Nonmetric multidimensional scaling plot in two dimensions of the similarity (Bray-Curtis) between bents (n = 8 quadrats within a bent) on date 9. Bents are represented by: bent 1 = open squares; bent 2 = open circles; bent 3 = closed circles; bent 4 = triangles; LP = closed squares. Stress = 0.19

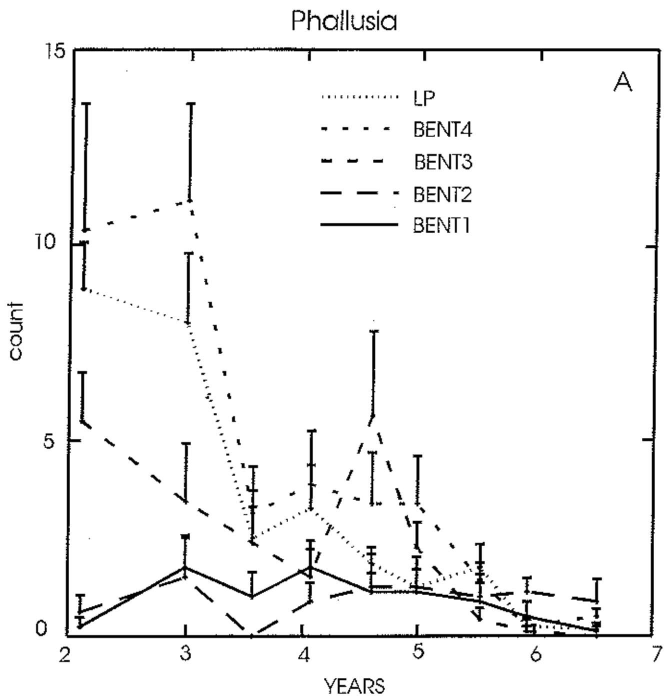
Dynamics of the Assemblage at Population Level

The first analyses of photographic data were done for date 1, July 1984. Sheet-, mound- and tree-form modular organisms, especially sponges and *T. multiflora*, were abundant by this time along with unitary organisms, especially bivalves and ascidians. Six years later this was still the case, although certain unitary organisms (*E. georgiana, O. angasi, A. trigonopsis*) had virtually disappeared and others (*P. obesa, Polycarpa* spp., *H. momus*) appeared to be declining (see below). The working hypothesis was that the modular forms would become progressively more dominant, overgrowing and displacing the unitary forms, but this occurred only slowly and to a limited extent.

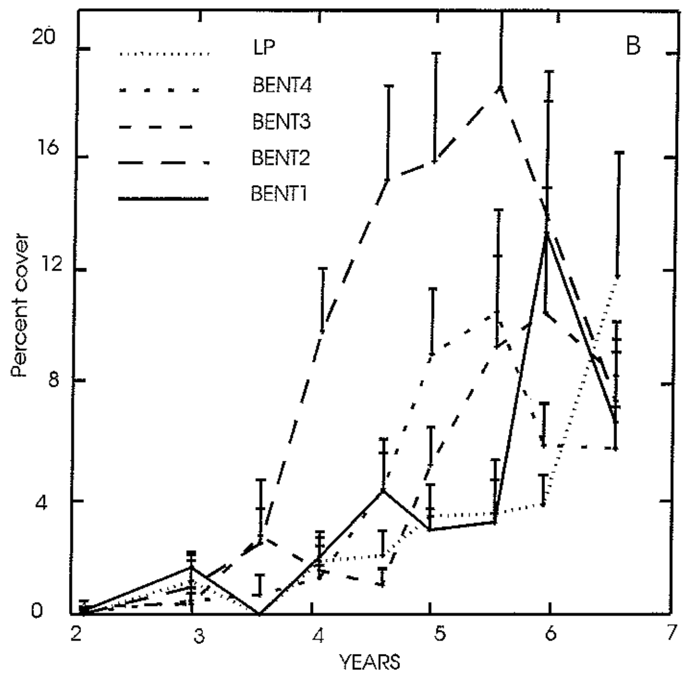
From the eighth visit, 10 July 1984, here labelled date 1, the trajectory of the biota can be described simply by plotting the means, for each of the five bents, of biological variables against time since the construction of the loading platform. These were plotted for 12 animal groups and for bare space. Examples are shown in Figure 4.

The behaviour of these 13 variables can be described under three categories:

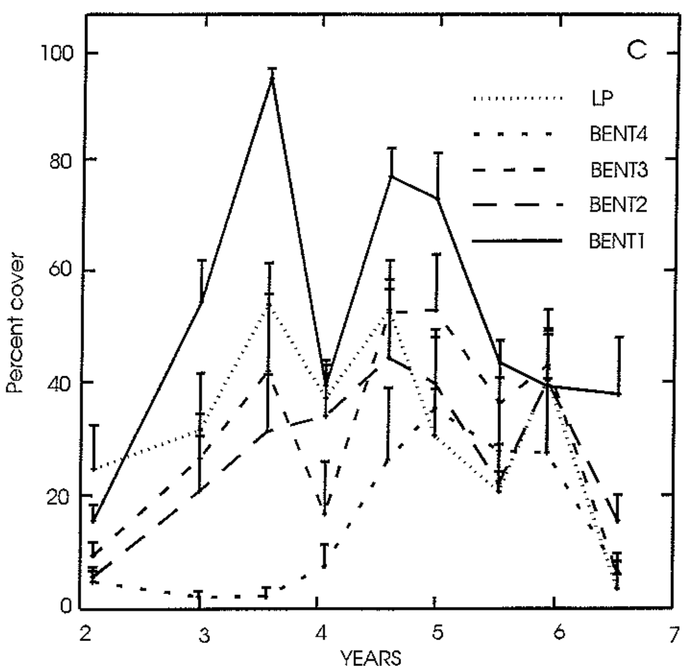
i. Species whose numbers appear to be generally falling through the 5-year period. These were *Triphyllozoon* sp., *P. obesa*, *Polycarpa* spp., *H. momus* and *Chlamys* spp. All but one are unitary organisms. The pattern is qualitatively the same for each of them, namely that numbers were always low at certain bents (not the same bents for different species, however) and initially high at others; numbers dropped through time at the bents where they had initially been high. The pattern is illustrated here by *P. obesa* (Fig. 4a).



White sponge



Telesto



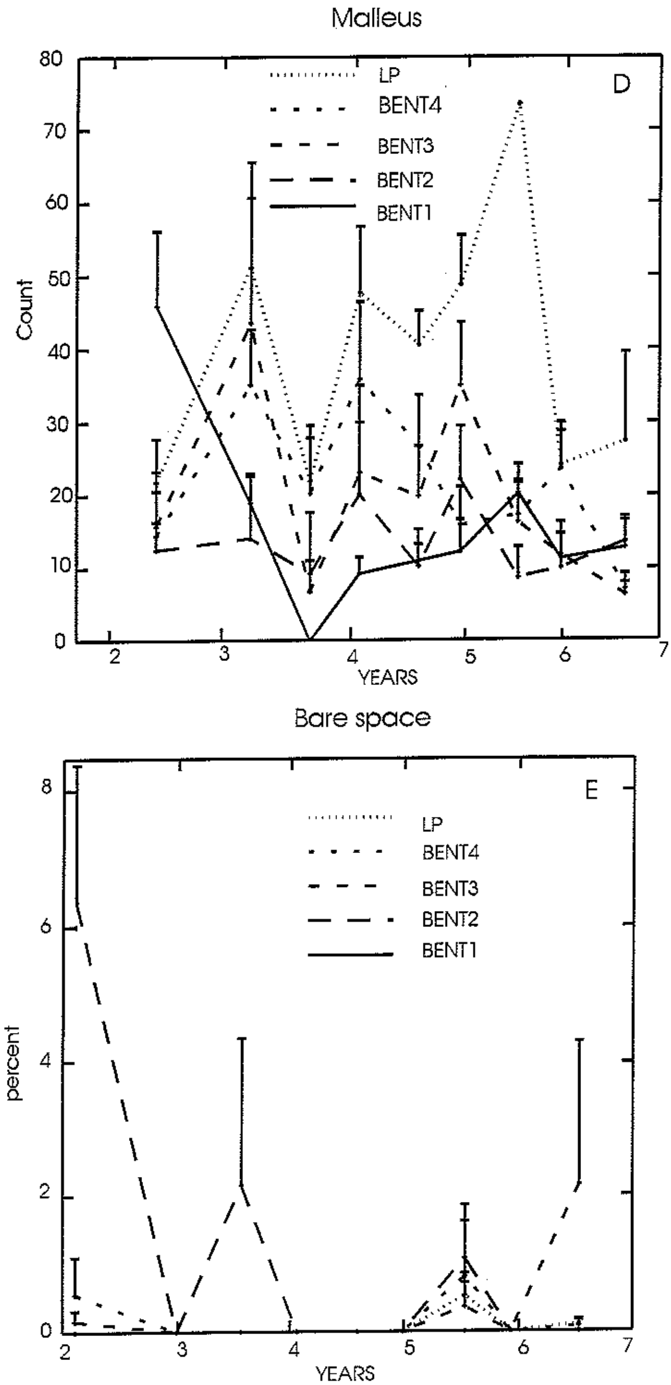


Fig. 4 Plots of single variables against time in years since the construction of the Loading platform. Bars are SE. A = *P. obesa* counts; B = White Sponge percent cover; C = *T. multiflora* percent cover; D = *M. meridianus* counts; E = percent of bare space.

ii. Species whose numbers appear to be generally rising through at least part of the 5-year period, though for some the rise has ceased or a decrease is detectable by the end of the study. These are all modular organisms: White Sponge, *H. disticha* (which also shows strong seasonal fluctuation, being more abundant in summer), *T. multiflora* and didemnid ascidians. This patterns illustrated here by White Sponge and *T. multiflora* (Figs 4b, 4c).
iii. Species for which there is no obvious trend, but wide variation between bents and through time. These include the bivalves *P. bicolor* (not generally considered a hard-substratum organism but consistently present on the pilings in low numbers) and *M. meridianus*, and the ascidians *Botrylloides* spp. (showing strong seasonal fluctuation, abundant in winter). The pattern is illustrated here by *M. meridianus* (Fig. 4d). Finally, bare space showed some fluctuations but was low throughout, commonly scoring zero at most bents (Fig. 4e).

It is difficult to recognise useful patterns in the graphs of single species on single bents against time because of the large variation in space and time and little consistency between bents. Figure 4 illustrates why species such as *P. obesa* (Fig. 4a), *T. multiflora* (Fig. 4c) and *M. meridianus* (Fig. 4d) were important contributors to the multivariate similarities between bents; there are some large differences between bents, but also between quadrats within bents (see the SE bars in Fig. 4) and the patterns vary greatly through time and differ between species. One interpretation of this is to say that even at the "bent" level (averaging over 8 quadrats, or 1.34 m^2), too small a spatial scale is being looked at and more "variation" than "pattern" is being seen. The multivariate view is probably more instructive.

Differences at Population Level between Bents after ca. Six Years

The approach chosen is first to make a multivariate analysis of the data using techniques that are robust to non-normality, small counts and many zeros. Then, since significant differences between bents were detected, variables which contributed strongly to them were examined. A small subset of those variables seemed to approximate the properties required for parametric analysis, and for five of them the pattern of difference between bents was examined using ANOVA on log (x + 1)-transformed data for date 9. As noted above, with fixed quadrats it is invalid to do analyses of variance using time as a factor (though the lack of independence may have little effect in practice, in the present case). Results are summarised in Table 3.

For most species, there is a significant bent effect, but not a significant effect of pile within bent. There is, however, nothing clear about the pattern of bents shown by the Tukey's test. Bent 4 and the LP tend to be high (*M. meridianus, Polycarpa* spp., *T. multiflora*) but this is not well-defined.

A multivariate analysis of variance (MANOVA) on the same 5 species gave qualitatively the same result, namely a bent effect significant at the 1% level, but no pile effect significant even at the 5% level. This is the same result as obtained (above) with a nonparametric multivariate analysis on a larger number of species.

Environmental Explanations

Five "environmental" variables which may have influenced patterns on the pilings were considered:

Treated ballast water outfall. Ballast water is released to sea from a 50 m long diffuser located near trestle bent 72, *ca* 1.8 km offshore, about 1 m above the seafloor in *ca* 10 m depth. The designed maximum contamination after treatment was 10 mg l^{-1} oil mixed in

Table 3 Nested analysis of variance on five variables from fixed quadrats on date 9, approximately 6.5 years after commencement of construction of the pier. N = the variable was a count; %C = variable was percentage cover. Values in table are probabilities of the F-values. On the right is the result of a Tukey's test for differences between means; numbers indicate bents and underlined groups are not significantly heterogeneous at the 5% level.

Variable	Effect of: Bent	Pile	Tukey test result
M. meridianus (N)	0.014	0.400	3 1 2 4 LP
Polycarpa spp. (N)	0.012	0.865	2 3 1 LP 4
T. multiflora (%C)	0.002	0.021	1 2 3 4 LP
H. disticha (%C)	0.006	0.268	1 2 LP 3 4
White Sponge (%C)	0.672	0.254	n/a

seawater. With the predicted dilutions in this high-current area, the result would be concentrations of 5–25 μg l^{-1} in the seawater near the diffuser. Bent 72 is midway between bents 2 and 3 as labelled here. Any impact of this outfall was expected to show as a gradient away from this point. In the MDS, bent 2 and to some extent 3 appeared more variable than others but this is difficult to discern in the univariate plots (see Fig. 4) and there is no clear trend away from these bents.

Current speed. Strong tidal currents associated with a gyre (Noye 1984, Noye *et al.*, 1994) centred on about bent 3 typically affect bents 1, 2, 4 and LP, whereas bent 3 is in an area of relatively slow moving currents. Any effects of current speed would therefore be partly confounded with those of the ballast water outfall. Indeed, in the pairwise comparisons following ANOSIM on abundance data for date 9, with Bonferroni adjustment, only pairs 1,3 and 3,LP were found to differ significantly. Thus there is some hint that current speed may be influential.

Shading at the LP. The high, narrow deck of the trestle does not shade the pilings at bents 1–4 as much as the wide deck and other complex structures and pipeworks do at the LP. Any effect would be seen as the LP standing apart from other bents in univariate or multivariate analyses, and it generally does not.

Depth (of the seafloor). This is about 15 m at bents 1–4, then increases sharply to 20 m at the LP. Effects would be partly confounded with shading at the LP, but there is no corresponding pattern in the results.

Disturbance from wave action. "Recently-cleared space" estimated *in situ* by divers at date 9 was analysed for differences between bents with either depth or direction as a second factor, using 2 two-factor ANOVAs. No effect of bent, direction or depth was found (Bent-Depth ANOVA: Bent, $P = 0.786$; Depth, 0.379; Bent × Depth, 0.063. Bent-Direction ANOVA: Bent, 0.803; Direction, 0.104; Bent × Direction, 0.677). There is therefore no prospect of wave action explaining differences in assemblages amongst bents.

DISCUSSION

The main concern of this paper is the development of the fauna through the 5–6 years following its initial, rapid colonisation, whether it reaches a homogeneous and "stable" condition and, if not, what environmental explanations might be offered. The working hypotheses were that the fauna on different groups of pilings would converge to some common composition dominated by modular organisms and that this common assemblage would represent a "stable" condition (showing little change with time; *cf* Kay & Butler, 1983; Keough & Butler, 1983). If the fauna on different groups of pilings did not reach a common composition, then the question would be asked which species contribute to similarities and differences between groups of piles, and indications would be sought of the possible effects of environmental variables.

Most studies of fouling assemblages, including the authors' earlier work in South Australia (Kay & Keough, 1981; Kay & Butler, 1983; Butler, 1986, 1991) have been done in sites where there is a substantial source of colonists in the form of "the mature fouling community" so close that even species having the most limited larval dispersal can reach the study substrata within one generation. In the present case, nearby sources of colonists were natural substrata which were small and of low profile. Even on brief inspections of them, the dominant species of the pilings were found on these natural substrata, but they were cryptic and in low abundance; the reefs were algal-dominated and did not bear the massive concentrations of certain species (*T. multiflora*, *M. meridianus*, solitary ascidians) that soon appeared on the pilings. Some sources were at small distances from the pilings; some *P. bicolor* were only metres from pilings, there is a low rock outcrop and boulderfield in 7–8 m depth about 500 m west of bent 24, and Point Lowly is only 1.9 km to the east. Indeed, unlike the other piers, different bents at Port Bonython are rather distant sources of colonists, each being 24 m, perpendicular to the prevailing current, from its nearest neighbour.

This is the sort of situation in which the piers at the authors' other study sites were established, but they were unable to observe their initial colonisation. There was no way to know whether "historical accidents" — the species that happened to be recruiting abundantly at the time—may have contributed to the composition of their fauna or how long any such effects may have persisted before the pilings became dominated by their present relatively stable and homogeneous faunas (Kay & Butler, 1983; Butler, 1986).

Establishment

It is not the main focus of this paper, but it is noted that the pier at Port Bonython was colonised rapidly. The LP and Bent 1 had 100% cover of 3-dimensional colonies, especially sponges on the LP, by mid-1983 when they were a little over one year old. Such an assemblage takes more than two years to develop at Edithburgh, Gulf St Vincent (Butler, unpublished observations). The differences might be attributed to high water movement and seasonally higher temperatures; both hypotheses are testable but cannot be addressed further with the present data.

Whatever the source of colonists, there was a very similar early trajectory at all bents at Port Bonython despite their different starting times, and within two years differences between bents were not such as to be attributable to age. Thus, "historical accidents" – seasonal pulses of particular species recruiting – have not contributed strongly to differences between bents after 2+ years.

Differences that would be accounted for by a model of early piles being colonised by species with long-distance larvae and later ones being colonised (perhaps more rapidly, or with a different initial species composition) directly from other piles of the pier were not observed. In particular, the composition of early assemblages observed on bents 2–4 was not like those already established on the older parts of the pier, but comprised species typically thought of as colonisers (*e.g.* hydroids) and species with long-lived planktotrophic larvae (*e.g.* bivalves).

The prediction that, following initial establishment of the assemblage, recruitment to bare space would henceforth be influenced by the standing fauna of the pier (and be relatively less dependent on long-distance larvae) is testable, but not with the present data. There is a huge area of the floor of the Gulf still in the state that prevailed off Stony Point before construction of the pier, current patterns are fairly well understood (Noye *et al.*, 1994) and recruitment could be measured near the pier and further away from its influence.

Composition

Before returning to the question of the development and "stability" of the fauna, a comment on its composition. Modular organisms were expected to become progressively more dominant, overgrowing and displacing the unitary forms, but this did not occur to the extent expected; indeed there was one reversal (sponges on bent 1 and the LP in the first year). Unitary animals, especially *M. meridianus, P. obesa* and *Polycarpa* spp., remained abundant after 6–7 years although the solitary ascidians appeared to have declined; encrusting and mound-form modular cover was still only modest and spatially variable, the rest of the space being occupied by unitary and arborescent forms.

It might be argued that the continuing abundance of unitary forms is due to the high current speeds and greater wave action experienced at this site, compared with other sites in Gulf St Vincent. Broadly, active suspension feeders tend to be advantaged at calm sites with low current speeds, but disadvantaged in areas of violent water movement if they are soft-bodied. In rougher conditions, tough tests like those of *P. obesa* or *T. multiflora* or shells like those of *M. meridianus* are advantageous, and passive filtering mechanisms like those of *T. multiflora* are adequate (*e.g.* Hiscock, 1983; Warner, 1984). In one sense the prediction was correct; throughout the present study, encrusting sponges and colonial ascidians persisted as a matrix through which *M. meridianus* and solitary ascidians protruded, whilst flatter unitary forms, *e.g.* serpulid worms, such as *Galeolaria* spp., oysters (*O. angasi*) and jingles (*A. trigonopsis*), were overgrown and eliminated.

Evidently, the conditions at Port Bonython are not severe enough to damage all soft-bodied modular forms; the category White Sponge prospered and increased in area covered throughout the study. It is difficult to compare rates of "disturbance" between sites because the measures integrate the effects of wave attack, substratum type and the characteristics of the biota. Bare space, for example, is low at Port Bonython compared with the undoubtedly more sheltered Edithburgh pier. An overall mean of divers' estimates of "recently-cleared space", as a measure of the rate of space-clearance, is 12.60% (n = 80, SEm = 2.104). For comparison, there are two kinds of estimates of "bare" space (showing the black piling surface). Underwater estimates made by divers on date 9 gave a mean of 0.67% (n = 80, SEm = 0.37). Estimates from photos on dates 7, 8, 9 pooled gave a mean of 0.35% (n = 116, SEm = 0.17). Bare space at Edithburgh remained in the order of 25% through two years (Kay & Butler, 1983). Perhaps substratum type is more important than wave action in determining the availability of bare space; the Edithburgh pilings are of timber, those at Port Bonython of epoxy-coated steel.

Port Bonython pier is cathodically protected against corrosion. There is evidence that cathodic protection can enhance the density and growth rate of macrofouling organisms such as barnacles and oysters (Eashwar *et al.*, 1995). The experiments of Eashwar *et al.* (1995) were done on small bare-metal coupons. Some parts of the likely explanation for the effects involve small-scale surface alterations and small-scale deposits on the metal surface; it is not known whether anything like these processes would occur on these large piles with their initial coating of coal-tar epoxy rather than bare metal. Part of the possible explanation, however, concerns the enhanced conditions for calcium deposition close to the cathodically protected surface, and it seems possible that this could be occurring on the jetty scale and could favour the growth of calcareous organisms (for example, *Malleus*). This must be left as one of the possible hypotheses that could contribute to an explanation for the differences between this pier and others studied, because there are no control surfaces of comparable size, surface properties and exposure to water movement but lacking cathodic protection. It is not obvious why increased calcification should favour organisms without calcareous skeletons but in the work of Eashwar *et al.* (1995) the recruitment and growth of certain algae, as well as calcareous animals, was enhanced under cathodic protection.

The slight decline in solitary ascidians and bryozoans and the rise in White Sponge suggests that the original prediction is being fulfilled but on al long timescale, and it might be suggested that certain early events were aberrations which merely delayed the eventual establishment of the predicted fauna. The die-off of mound-forming sponges from bents 1 and LP after the first year suggested that the prediction was wrong, but might be seen as a "species-selection" of forms adapted to the local conditions. Local physical or nutritional conditions are clearly important, in addition to any more general mechanism. Hydroids, certain bivalves and solitary ascidians have remained more abundant at Port Bonython than at Edithburgh and Rapid Bay, whilst the faunas of those two piers remain different from one another (Kay and Butler, 1983; Butler, 1986). It is noteworthy that Schmidt (1983) documented the enhancement of settlement of solitary ascidians by a canopy of the hydroid *Tubularia larynx*; Schmidt cites other examples, and it is possible that hydroids enhanced ascidian recruitment here, leading to a dominance by those organisms that is only slowly decreasing. The hypotheses indicated in the preceding paragraphs are all testable, notably by transplant experiments.

Dynamics

Despite their very similar early trajectories, the assemblages on the five bents spaced along the pier remain significantly different, although they seem to have been moving roughly "in parallel" in multivariate space over the 5 year period. By the end of the study the rate of change seemed to be slowing down, judging by the univariate plots. It might be tempting to say that the community was becoming "stable", but this is an elusive concept. It has variously been argued that "stability" means little unless data are gathered over a timescale longer than a generation span or even the maximum lifespan of the dominant or important species (*e.g.* Connell & Sousa, 1983), and the lengths of life of, *e.g. M. meridianus, Polycarpa* spp., or a *T. multiflora* colony are not known. There are "stability" concepts which are useful with respect to stochastically-varying ecological systems and which refer to the extent of fluctuations or times to particular events. For example, Keough and Butler (1983) and Kay and Butler (1983) used the idea of "narrow stochastic boundedness" of a randomly varying quantity. That test has not been formally applied here because it is clear by visual inspection (*cf* Kay & Butler, 1983; Keough & Butler, 1983 with Fig. 4 here) that the present data would fail the test. The relative abundances of species at Port Bonython, viewed at a "quadrat" scale, are spatially patchy and fluctuate widely through time. Even bents were significantly different at date 9 but not in consistent ways through time (from the univariate data) nor with simple explanations in terms of the contributing species; the pier might be taken to be "patchy" on a "bent" scale also.

Some of the variation recorded here could be an artifact, due to the propensity of the random-dot technique to either under-estimate or over-estimate rare species, depending whether it happens by chance to hit or miss them (Dethier *et al.*, 1993), and also because of the arborescent nature of *T. multiflora* which means that it obscures other species variably. It is not thought, however, that these factors are likely to be of major importance here because the fluctuations are observed in common species, because direct visual estimates of bare space do not differ widely from dot-counted estimates, and because there was no evidence that counts were worse where *T. multiflora* was more common.

The community may be tracking towards the "narrowly stochastically bounded" situation characteristic of several sites in Gulf St Vincent (Kay & Butler, 1983), but has not displayed it over its first seven years. (It is not known how long it took to be established at the other sites). An appropriate test would be to resurvey the pier after a further six to eight years; the prediction from the above qualitative model would be that bents would differ from one another and each bent would differ from its condition in 1989 but that the pier as a whole would not be strongly different from 1989; a two-way ANOSIM (factors date with two levels and bent with five levels) should find significant bent effects overall, little overall date effect but a significant interaction between date and bent, evidenced by clear bent effects at some dates but not others. An alternative model is that the bent differences are not merely "noise" but reflect environmental differences between bents, such as the differences in current speed which may account for differences between bent 3 and bents 1 and LP in the multivariate analyses. This model would predict that on a future visit not only would the composition of the assemblage over the whole pier be found to be similar to that on date 9 but also each bent would be similar to its composition then, and bents would differ in the same ways; a two-way ANOSIM (date-bent) should find a significant bent effect but no significant date effect nor implied interaction, from examining the separate 1-way ANOSIM tests.

Short-term variation of the kind observed here has been recorded in other sessile communities (*e.g.* Chiappone & Sullivan, 1994) and, without any basis for comparison, it cannot be known whether to attribute it to "natural fluctuations" or to a low level of "stress" (*e.g.* minor spills and use of dispersants affecting the whole length of the pier or perhaps different events affecting different points along the pier).

Further Testing

The overall model for the dynamics of this sort of assemblage is complex and not testable as a single hypothesis, but components of it can be tested, and some of them have been noted above; they include the effects of water movement and temperatures on colonisation, the effects of current speed and wave action on the relative abundance of unitary forms, and the effects of cathodic protection on the composition of the fauna. It is thought, however, that the most interesting questions, and most likely of general application, concern the extent to which colonisation of bare space is influenced by the standing fauna of the pier (and relatively less dependent on long-distance larvae), and whether the assemblage on the pier as a whole is tracking towards the same "narrowly stochastically bounded" composition or whether bents will remain different. These questions have implications not only for fouling management but also for general ecological theory.

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