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Patterns of higher taxon colonisation and development in sessile marine benthic assemblages at Casey Station, Antarctica, and their use in environmental monitoring

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ABSTRACT: Colonisation and development of sessile epibiotic assemblages on tiles was studied at Casey Station, East Antarctica, using a mix of higher taxon classifications (family to phylum). Tiles were deployed for 1 and 3 yr at 3 control and 2 impacted locations. Assemblages on upper and lower surfaces of tiles were very different, with little colonisation of upper surfaces (0 to 11% after 3 yr) and extensive colonisation of lower surfaces (60 to 91% after 3 yr), which is greater than previously reported from Antarctica. Hypotheses were tested relating to spatial variation, depth, human impacts (a sewage outfall and a waste disposal site) and period of deployment. Differences between control locations were only apparent after 3 yr, but there were significant differences between control and impacted locations after 1 yr. There were differences between assemblages at 7 to 10 m and 19 to 22 m. Assemblages were initially dominated by spirorbid polychaetes and bryozoans, but by 3 yr there was significant sponge cover at some locations. Both impacted locations had significantly greater cover on upper surfaces than controls. The waste disposal site had the least cover on lower surfaces, with almost no sponge and less bryozoans than controls. The outfall had the greatest cover on the lower surfaces, the greatest cover of spirorbids and sponges but the least cover of bryozoans. Higher taxa assemblage patterns of colonisation on settlement panels are potentially useful as a medium- to long-term monitoring tool for sheltered Antarctic nearshore waters.

KEY WORDS: Marine benthos · Colonisation · Settlement panels · Environmental impact · Assemblage succession · Monitoring

INTRODUCTION

Settlement panels provide an ideal tool for investigating ecological patterns and processes of sessile encrusting epifauna in benthic ecosystems (e.g. Stachowicz et al. 2002). They have been used to study environmental impacts in temperate environments, for example of marinas (Glasby 1997, 1998), and the role of urban structures as marine habitats (Connell 2001). They reduce heterogeneity associated with natural substrata, provide a degree of uniformity and facilitate replication, which is essential to estimate natural variation in comparisons of different areas. Studies of developing epibiotic assemblages in temperate areas have found significant spatial variation at scales from 10s to 1000s of m (Keough 1983, Butler 1986, Glasby 1998), but settlement panels are also suitable in tests for differences and patterns at local scales (Glasby 1998), making them useful in impact assessment and monitoring.

Environmental impact studies in near-shore habitats commonly focus on assemblages of soft-sediment macrofauna, largely because sediments accumulate contaminants (Goldberg et al. 1975, Stark et al. 2003b). Less common is the use of assemblages on hard substrata, which provide different ecological information, as they are less likely to be affected by accumulated contaminants in sediments. Their development is more responsive to short-term or periodic environmental changes, such as waterborne pulsed pollution events,

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which may occur when contaminants are introduced or resuspended. The few previous studies of epibiotic assemblage development on hard substratum in Antarctica have reported very low colonisation rates (Dayton 1989, Rauschert 1991, Barnes 1996, Stanwell-Smith & Barnes 1997). Recently, however, Bowden et al. (2006) reported faster colonisation rates in Antarctica with assemblage development that was highly location-specific in terms of both composition and abundance, with significant spatial variability at scales of <5 km, and also influenced by depth.

There is a need for techniques suitable for monitoring the impact of anthropogenic activities like sewage release and waste disposal on the Antarctic environment. Antarctic stations established before the late 1980s disposed of waste in convenient landfill sites, often close to shorelines. Abandoned waste disposal sites pose environmental threats to marine ecosystems through runoff and leaching of contaminants into the sea during summer melt periods, creating pulsed pollution events. The effects of these waste disposal sites has become a recent focus of research in areas of Antarctica (Lenihan 1992, Lenihan & Oliver 1995, Stark et al. 2003a,b, 2004, 2005), but this research has focused exclusively on soft sediments. There has also been research into the effects of sewage outfalls on soft sediments in Antarctica (Green & Nichols 1995, Conlan et al. 2004). Research at Casey Station has shown conclusive evidence of environmental impacts of a waste disposal site and the sewage outfall in soft sediments (Stark et al. 2003a,b, 2004). However, there are no published studies of environmental impacts on benthic assemblages in hard substratum habitats in Antarctica, and settlement panels have not been used there for environmental monitoring or impact assessment.

Fauna in soft sediments exhibit a range of responses to certain types of stressors, some of which can be characterised at higher taxonomic levels, e.g. polychaetes and organic contamination (Pearson & Rosenberg 1978). Despite species-level differences within a taxon in response to environmental influences, it has been clearly demonstrated that there are generalized higher-level taxon responses to certain stressors (such as pollution), some of which are apparent even at the phylum level (Lenihan et al. 2003). These higher-taxon responses are generally driven by particular species or families within the taxon, for which there may be contrasting responses for other species or families within the same taxon (Lenihan et al. 2003). This does not invalidate the higher-taxon pattern that is observed in response to a stressor. Whether the actual cause is direct (e.g. sensitivity to pollution) or indirect (e.g. a release from predation), such characteristic patterns can be valuable, e.g. in a monitoring context. These quantitative observations not only provide the context and basis for further understanding of the mechanisms and processes responsible (Underwood et al. 2000), but also provide important information in their own right. Many studies have demonstrated little loss of information by analysing data at higher taxonomic levels, even phylum (Warwick 1988, Somerfield & Clarke 1995, Olsgard et al. 1998), but even where species level patterns may be different, important information can be gained at higher levels. Working at higher levels may also reduced the noise and variability associated with signals at species level (Warwick 1993). Additionally, the concept of identifying organisms to a level sufficient to meet a study's objectives, such as for environmental monitoring, or to streamline sample processing is well known (Ellis 1985, Anderson et al. 2005). Responses of biota on hard substrata to pollution at higher taxononomic levels are less well known than in sediments, but they have been shown to exhibit clear patterns in response to other environmental variables from family level, e.g. spirorbid polychaetes (Glasby & Connell 2001), up to phylum level, e.g. sponges (Glasby 2001). While species identifications are important to certain ecological questions, the extent to which assemblage patterns at higher taxonomic levels relate to environmental influences warrants further investigation (Anderson et al. 2005).

The aim of this study was to determine whether there were general patterns of colonisation and development of Antarctic sessile benthic assemblages apparent at higher taxonomic levels, using coarse resolution of family, morphospecies/functional groups and phylum and to determine how useful these might be for environmental monitoring. Five hypotheses were tested relating to assemblage development on tiles: (1) spatial—that there would be differences in assemblages at scales of several km (between locations), and at 10 to 50 m (between sites within locations); (2) impact—that there would be differences between impacted locations (adjacent to a waste disposal site and a sewage outfall) and control locations; (3) depth—that there would be differences between depths within locations; (4) temporal—that there would be differences between assemblages at 1 and 3 yr; and (5) variability—that there would be differences in the variability of assemblages between control and impacted locations.

MATERIALS AND METHODS

Study area. Casey Station (66° 17′ S, 110° 32′ E) is in the Windmill Islands, East Antarctica (Fig. 1a,b). Low rocky hills and ice cliffs border several bays around Casey, which contain smaller, inner bays. Sea ice cover

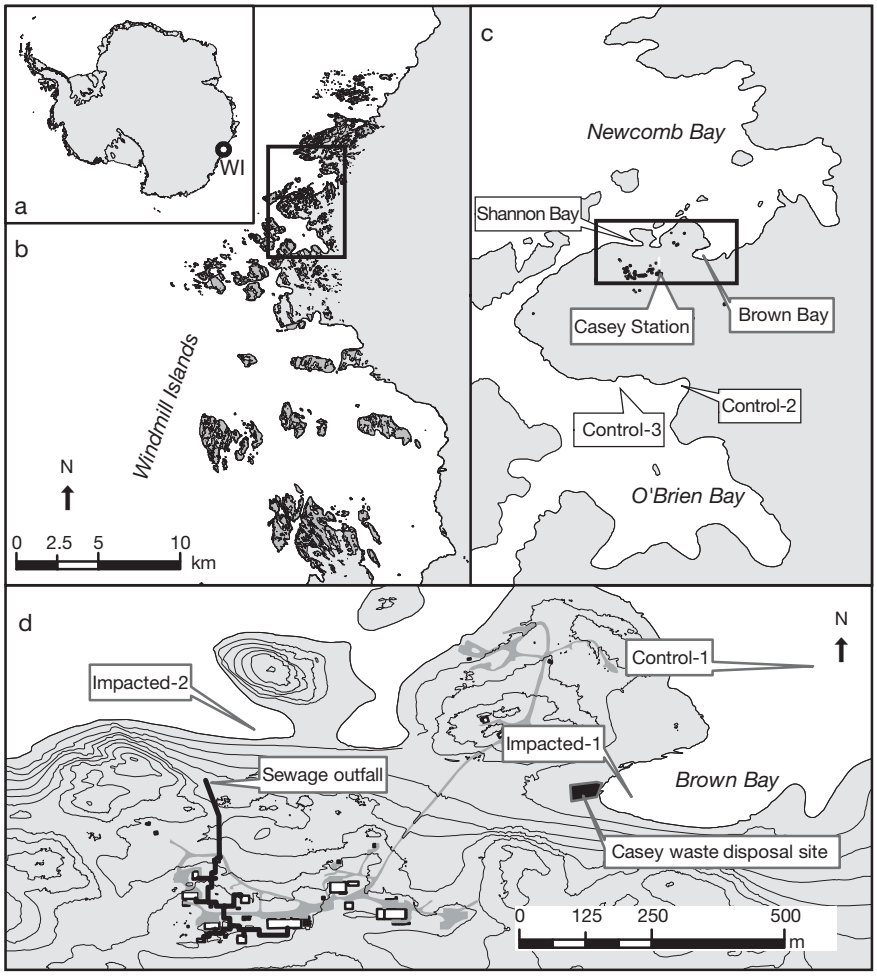

Fig. 1. (a) Windmill Islands (WI) region in Antarctica; (b) Casey station area (boxed) in the Windmill Islands; (c) Casey Station and the tile deployment locations; (d) Casey Station and the deployment locations (Impacted-1, Impacted-2, Control-1) near the sewage outfall and waste disposal site

in these bays is 1.2 to 2 m thick, and breakout at the sites in this study occurs between December and February in most years.

The old Casey waste disposal site is in Thala Valley, 450 m northeast of Casey Station, adjacent to Brown Bay (Fig. 1d). Waste material was dumped at the seaward end of Thala Valley and directly into the bay between 1969 and 1986 (Deprez et al. 1999, Snape et al. 2001). During summer, melt water from the surrounding slopes runs through the valley and percolates through the site, entraining contaminants before entering the marine environment and depositing them in Brown Bay (Snape et al. 2001). Sediments in Brown Bay are contaminated by metals and hydrocarbons (Stark et al. 2003b).

The Casey sewage outfall discharges secondary treated and occasionally primary treated sewage ca. 40 m from the edge of Shannon Bay into the ice cliff. Heated sewage has melted a hole in the ice down to the rock ~5 m beneath, where it follows an unknown path for 10s of m into Shannon Bay. A pilot study indicated that there was a distributed discharge along the shore of Shannon Bay rather than a point source, with significant levels of ammonia, phosphorous and bacteria in the water column (Morris et al. 2000).

Materials. The settlement panels consisted of unglazed porcelain tiles (15 × 15 cm), with a slightly textured upper surface and 3 × 3 cm slightly raised grid (~1 mm high) on the lower surface. Two tiles were attached 10 cm apart with silicon to the top edge of a trough made from one-half of a 40 cm long, 15 cm diameter stormwater pipe (Fig. 2a). The ends of each trough were open, leaving a semi-cylindrical cavity under each tile. Thus, the upper and lower surfaces were both exposed to predation and currents. The pipe was attached to the top of a mesh bag containing rocks as ballast and the tube was positioned horizontally on the seabed. After collection, the tiles

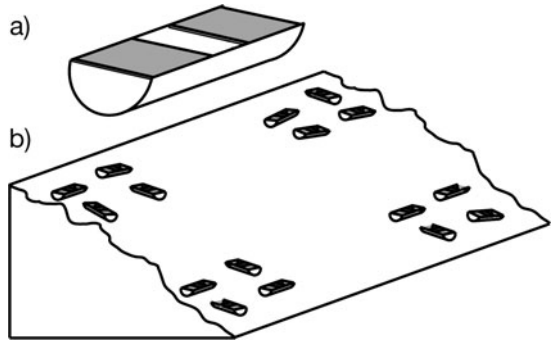

Fig. 2. (a) Two tiles were situated in the top of a trough formed from one-half of a PVC pipe; (b) Experimental design at each site showing groups of 8 tiles, 2 shallow sites and 2 deep sites. At Impacted-1 and Control-1 there was no depth comparison (the seabed was flat) but the layout was the same to test for spatial differences

were photographed using a high-resolution (5 megapixel) digital camera while the organisms were still alive and then preserved in alcohol for a future study of species-level patterns. A grid of 100 evenly spaced points, excluding the outer 1 cm of each tile, was overlain on the photographs of the upper and lower surfaces of each tile and the biota directly under each point was identified using the categories of taxon shown in Table 1.

Experimental design. Tiles were deployed and collected by divers at 5 locations. Two locations were adjacent to sources of contamination and are known to have contaminated sediments and disturbed soft-sediment communities (Stark et al. 2003a, Stark et al. 2003b): Impacted-1 was in Brown Bay, ~50 m from the waste disposal site; Impacted-2 was in Shannon Bay, ~100 m from the sewage outfall (Fig. 1c,d). There were 3 uncontaminated control locations: Control-1 was in the outer part of Brown Bay, ~500 m from the waste disposal site; Control-2 and Control-3 were in O'Brien Bay, south of Casey Station (Fig. 1c). Tiles were deployed at 2 depths at each location (7 to 10 m and 19 to 22 m) except at Impacted-1 and Control-1. At each depth, tiles were deployed at 2 sites ~20 m apart in groups of 8 tiles (4 troughs ~1 to 2 m apart), for a total of 32 tiles at each location (Fig. 2b). It was not possible to deploy deep tiles at Impacted-1, as there is no deep habitat near the waste disposal site, nor was it possible to deploy shallow tiles at Control-1. However, at these 2 locations, 2 groups of 8 tiles (in plots of 4 troughs) were placed ~50 m apart to examine small-scale spatial variation. Tiles were deployed between 15 November and 31 December 1997. Tiles were collected after 1 yr (between 1 and 23 February 1999) and 3 yr (between 13 and 19 December 2001). One tile was collected from each of 2 randomly selected pipes at each site/depth at each sampling time (a total of 8 per location). Some tiles could not be retrieved, including 2 tiles at Impact-1 during the first collection, and all tiles at Control-2 and 2 tiles at Control-3 during the second collection.

Statistical analyses. Tests of multivariate null hypotheses of no differences among *a priori* defined groups were done using analysis of similarities (ANOSIM, Clarke 1993) in PRIMER-6 (Plymouth Marine Laboratory). Similarity matrices were based on the Bray-Curtis similarity measure on arcsin of square-root ($\sin^{-1}\sqrt{prop}$) transformed proportional cover. This has the effect of decreasing the weighting of very abundant taxa and increasing the weighting of very rare taxa, with little effect on mid-range proportions (Quinn & Keough 2002). Many studies have used fourth root transformed percentage cover of taxa (e.g. Glasby 2001, Glasby & Connell 2001); how-

Table 1. Taxonomic categories used in analysis of tiles

	Description
Upper surfaces	
Diatoms	Biofilm consisting mainly of diatoms
Macroalgae	Red macroalgae only, not possible to identify from basal growths
Spirorbids	All dextral coiling (clockwise spiral)
Sponge	Very little sponge recorded on upper surfaces, mainly *Homaxinella* sp.
Encrusting bryozoan	Flat, prostrate cheilostomate colonies
Lower surfaces	
Macroalgae	Red macroalgae only
Spirorbids	All dextral coiling (clockwise spiral)
Encrusting bryozoans	Flat, prostrate cheilostomate colonies
Branching bryozoans	Upright, branching cyclostomate bryozoan, mainly *Hornera* sp.
Round bryozoans	Uniformly round, domelike colonies
Lumpy bryozoans	Encrusting but not prostrate, lumpy in appearance, mainly *Beania* sp.
Sponge 1	White/beige small tube-forming sponge
Sponge 2	Beige spiky sponge
Sponge 3	White encrusting sponge
Sponge 4	Orange encrusting sponge
Eggs	Possibly gastropod eggs
Hydroids	Feather-like thecate hydroids
Terrebellids	Tube-building terrebellid polychaetes
Ascidian 1	Clear, colourless ascidian
Ascidian 2	Pale green ascidian
Unidentifiable	All other organisms unidentifiable from photos

ever, this is an extreme transformation for percentage cover data, which essentially reduces abundances into 4 categories. Relationships between samples were represented graphically using non-metric multidimensional scaling (nMDS) ordinations. Taxa contributing to differences between groups were determined using similarity of percentages analysis (SIMPER, Clarke 1993). A test for small-scale spatial variation was done at 2 locations, Impacted-1 and Control-1, where no depth comparisons were possible but the additional sites provided the replication necessary for an ANOSIM test for differences between sites. Where multiple comparisons were made, the significance level used was adjusted using the sequential Bonferroni correction (Rice 1989). Differences in the variability of assemblages were tested using the program PERMDISP2 (Anderson 2004), which compared the multivariate dispersions among groups on the basis of Bray-Curtis dissimilarity. The test calculates the distances from observations to their group centroids and compares the average of these distances among groups, using ANOVA (Anderson 2006). A p-value is then obtained using permutations of the observations.

Univariate analyses were done using ANOVA on percentage cover of major space occupants. Data were analysed by a 3 factor design, with Time (T), Location (L) and Depth (D) as fixed, orthogonal factors. Cochran's *C*-test was used to test for homogeneity of variances and, where heterogeneous, data were transformed (Underwood 1981). Where heterogeneity of variances could not be removed by transformation and were significant at p = 0.05, a probability level of p = 0.01 was used. Multiple comparisons among means were done using the Student-Newman-Keuls test (SNK test). To balance the ANOVA for missing tiles, the averages of the other locations (for the missing location Control-2 at 3 yr) and the mean of the 6 collected tiles at Control-3 were substituted in the analyses and the number of degrees of freedom of the residual was reduced in the ANOVAs (Underwood 1981). Several comparisons were ignored in post-hoc tests of means (SNK), as they were not possible to make, including comparisons of depth at Impacted-1 and Control-1 or comparisons involving Control-2 at 3 yr.

RESULTS

Assemblage composition

There were major differences in the assemblages recruiting to the upper and lower surfaces of the tiles. Upper surfaces were partially covered by a mixture of semi-consolidated sediment (from 12 to 55% mean cover), which washed off during processing, and a film of diatoms (from 0 to 59% mean cover) (Fig. 3a,b). The sediment on tiles was heavily colonised by tanaid crustaceans at some locations, and upper surfaces also had many micro-gastropods. The amount of sedimentary material differed little between locations, times and depths, the only significant difference being at Control-2 after 1 yr, where the sediment was almost double that at other locations (ANOVA: T × L, MS = 1417, $F_{4,48}$ = 4.7, p = 0.003; SNK: p < 0.01, Fig. 3a). The diatom film was significantly different between locations and times and decreased in the following order after 1 yr: Control-3 = Control-1 > Control-2 = Impacted-2 > Impacted-1 (ANOVA: T × L, MS = 1907, $F_{4,48}$ = 11.6, p < 0.001; SNK: p < 0.01, Fig. 3b). By 3 yr, there was very little primary diatom cover on upper surfaces at any location (Fig. 3b).

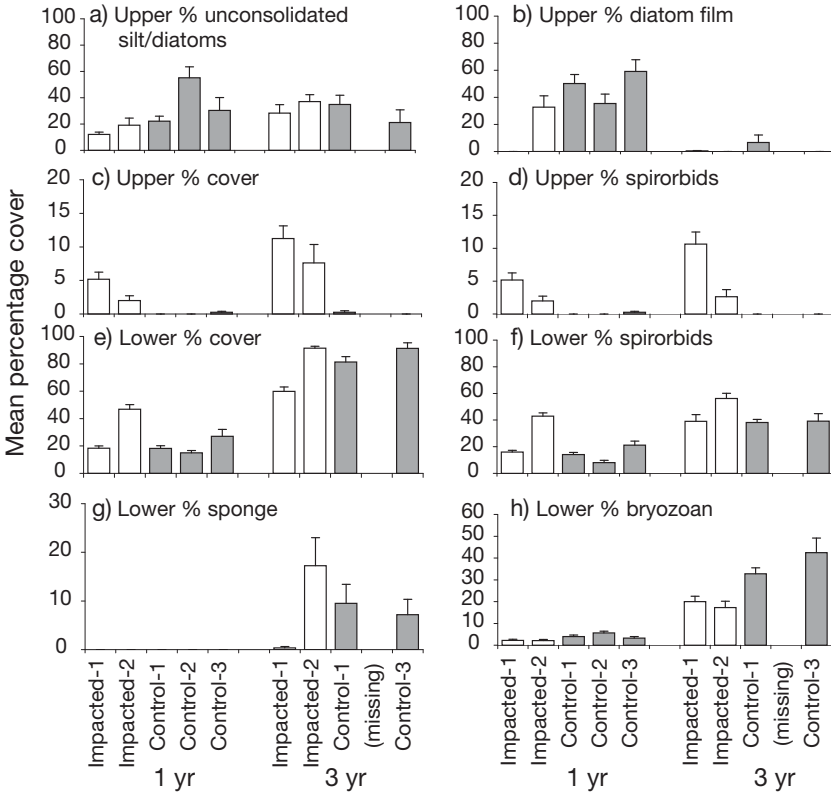

Fig. 3. Mean percentage cover (+SE) of major groups of sessile organisms at each location at 1 and 3 yr. White bars represent impacted locations

Total cover of sessile organisms on upper surfaces (excluding diatoms) ranged from 0 to 5% after 1 yr and 0 to 11% after 3 yr (Fig. 3c) and consisted mainly of spirorbid polychaetes (Fig 3d). There were significant differences between locations, with Impacted-1 having significantly greater cover than Impacted-2, which was greater than all other locations at both times (SNK: $p < 0.01$, Table 2a, Fig. 3c). Total cover on the upper surfaces also increased significantly at the 2 impacted locations from 1 yr to 3 yr (SNK: $p < 0.01$, Table 2a, Fig. 3c), but composition differed, with Impacted-1 consisting mainly of spirorbid polychaetes (1 yr = 5.2%, 3 yr = 10.6%) and Impacted-2 shifting from spirorbids to macroalgae (1 yr = 2% spirorbids; 3 yr = 2.6% spirorbids, 5% macroalgae). Little was found growing on the upper surfaces at other locations (Fig. 3c).

Biotic assemblages on the lower surfaces occupied between 15 and 47% mean total cover after 1 yr and between 60 and 91% after 3 yr and consisted almost entirely of spirorbids, bryozoans and sponges (Fig. 4). Bare space was predominant at 1 yr and spirorbids were the dominant colonist, but by 3 yr bryozoans and sponges were significant components of the assemblage and there was little remaining unoccupied space, except at Impacted-1 (Fig. 4). Total percentage cover on the lower surfaces was significantly greater at 3 yr at all locations (SNK: $p < 0.01$, Table 2b, Fig. 3e). There were significant T × L interactions in lower total % cover: at 1 yr Impacted-2 > Control-3 > all others (SNK: $p < 0.05$ Table 2b, Fig. 3e); at 3 yr there were fewer differences in total cover, with Control-3 and Impacted-2 > all others, and Impacted-1 < all others (SNK: $p < 0.05$, Table 2b, Fig. 3e). The only effect of depth on total lower cover was at O'Brien-3, which had greater % cover at deep sites at 1 yr and greater % cover at shallow sites at 3 yr (T × L × D interaction, SNK: $p < 0.05$, Table 2b).

Percentage cover of spirorbids on the upper surfaces was greatest at the 2 impacted locations, with very little recruitment at the other locations (Table 2c, Fig. 3d). On the lower surfaces, spirorbid cover ranged from a mean of 8 to 43% after 1 yr, and after 3 yr was very similar at Impacted-1, Control-1 and Control-3

Table 2. Results of 3-factor ANOVA testing for differences in cover of major taxa between times, locations and depths. df: degrees of freedom; MS: mean square estimates; *C*: Cochran's *C*-test result; untrans: data not transformed; sqrt: square root; NS: not significant. Significant results in **bold.** *F* versus Residual in all cases

Source	df	MS	*F*	p	MS	*F*	p
(a) Upper % cover (ln_{x+1}), ($C = 0.33$, $p < 0.01$)					**(b) Lower % cover (untrans), ($C = 0.18$, NS)**		
Time	1	8.61	46.04	**<0.0001**	62435.66	1534.27	**<0.0001**
Location	4	11.94	63.84	**<0.0001**	2108.44	51.81	**<0.0001**
Depth	1	0.06	0.34	0.56	152.17	3.74	0.059
Time × Location	4	2.23	11.93	**0.0001**	559.15	13.74	**<0.0001**
Time × Depth	1	0.05	0.28	0.6	143.11	3.52	0.067
Location × Depth	4	0.14	0.76	0.56	112.96	2.78	0.037
Time × Location × Depth	4	0.05	0.29	0.88	329.95	8.11	**<0.0001**
Residual	48	0.19			40.69		
(c) Upper spirorbids (ln_{x+1}), ($C = 0.34$, $p < 0.01$)					**(d) Lower % spirorbids ($sqrt_{x+1}$), ($C = 0.23$, $p < 0.05$)**		
Time	1	3.05	26.27	**<0.0001**	94.10	265.63	**<0.0001**
Location	4	11.00	94.84	**<0.0001**	13.31	37.59	**<0.0001**
Depth	1	0.42	3.58	0.065	0.93	2.63	0.11
Time × Location	4	1.76	15.20	**<0.0001**	4.44	12.53	**<0.0001**
Time × Depth	1	0.45	3.87	0.055	2.57	7.25	**0.01**
Location × Depth	4	0.19	1.66	0.18	0.79	2.22	0.08
Time × Location × Depth	4	0.55	4.74	**0.003**	2.22	6.26	**0.0004**
Residual	48	0.12			0.35		
(e) Lower % sponge ($sqrt_{x+1}$), ($C = 0.36$, $p < 0.01$)					**(f) Lower % bryozoan ($sqrt_{x+1}$), ($C = 0.21$, NS)**		
Time	1	58.93	247.39	**<0.0001**	209.00	615.01	**<0.0001**
Location	4	3.96	16.64	**<0.0001**	5.45	16.05	**<0.0001**
Depth	1	10.93	45.88	**<0.0001**	0.10	0.28	0.6
Time × Location	4	3.96	16.64	**<0.0001**	2.68	7.90	**<0.0001**
Time × Depth	1	10.93	45.88	**<0.0001**	1.16	3.43	0.07
Location × Depth	4	2.49	10.44	**<0.0001**	0.99	2.93	**0.03**
Time × Location × Depth	4	2.49	10.44	**<0.0001**	0.77	2.27	0.075
Residual	48	0.24			0.34		

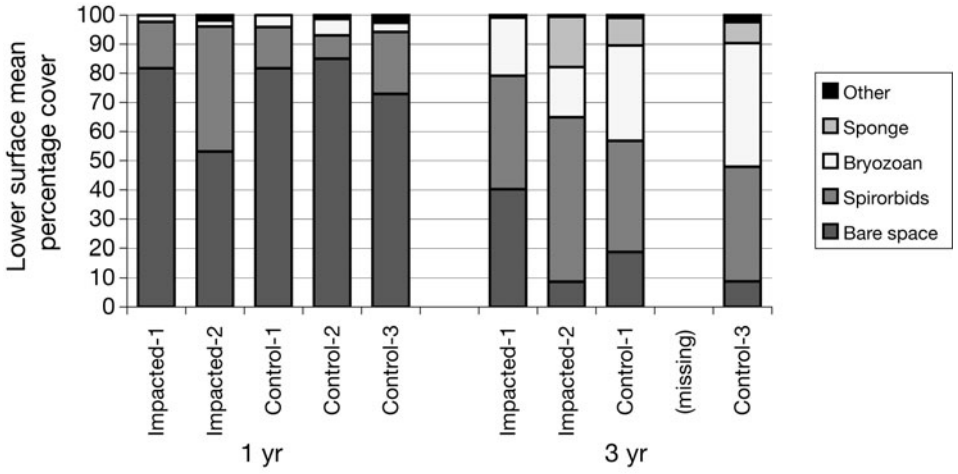

Fig. 4. Relative proportion of major taxa on lower surfaces of tiles at each location at 1 and 3 yr

(mean ~39%), with a mean of 56% cover at Impacted-2 (Fig. 3f). Spirorbid cover was significantly greater at Impacted-2, the sewage outfall (Fig. 3f), than all other locations at both times (T × L, SNK: $p < 0.05$, Table 2d). There was no consistent pattern of spirorbid recruitment in relation to depth.

Almost no sponge cover was recorded after 1 yr, but by 3 yr there had been significant recruitment on lower surfaces (Fig. 3g). Recruitment was lowest after 3 yr at Impacted-1 (mean 0.37%) and highest at Impacted-2 (mean 17.25%) (T × L, SNK: Impacted-2 > Control-1 = Control-3 > Impacted-1, $p < 0.01$, Table 2e). At the 2 sites where a depth comparison was possible (Impacted-2 and Control-3) there was significantly greater sponge cover on tiles at the deep sites (T × L × D, SNK: deep > shallow at both locations, $p < 0.01$, Table 2e).

Bryozoan cover on the lower surfaces ranged from 2 to 6% at 1 yr and 17 to 43% at 3 yr, and was least at both impacted locations at 1 and 3 yr (Fig. 3h). At 1 yr the only significant difference was that Control-2 had greater bryozoan cover than Impacted-1 (T × L, SNK: $p < 0.05$, Table 2f). After 3 yr there were significant differences among locations with Control-3 > Control-1 > Impacted-1 = Impacted-2 (T × L, SNK: $p < 0.01$, Table 2f). There were no significant differences between depths.

Assemblage patterns

Most hypotheses were supported, with clear assemblage patterns related to spatial effects, human impacts, period of deployment and depth, which can be seen in nMDS ordinations of the combined upper and lower surfaces (Figs. 5 to 7). There were no significant differences in assemblage variability at this higher-taxon level.

Spatial patterns

Control locations were not significantly different at 1 yr, but they were by 3 yr (Table 3), although Control-2 was not sampled at this time. The overlap of control samples in the nMDS apparent at 1 yr is clearly not evident at 3 yr, when distinct separation is seen (Fig. 5). Differences between Control-1 and Control-3 were mainly due to the different bryozoan categories, with particular forms more abundant at one location. SIMPER analysis indicated that there were large differences in cover of branching bryozoans and lumpy bryozoans, both of which are thought to represent single species. At the 2 locations where within-location, small-scale spatial variation

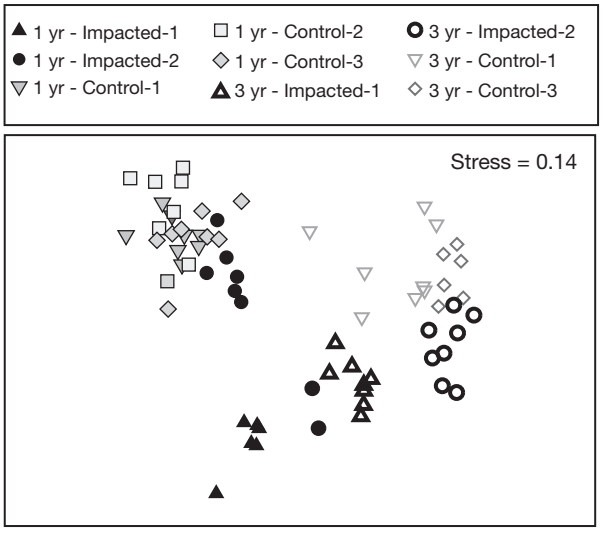

Fig. 5. Non-metric multidimensional scaling (nMDS) ordination of assemblages (combined upper and lower surfaces) on each tile at each location at 1 and 3 yr

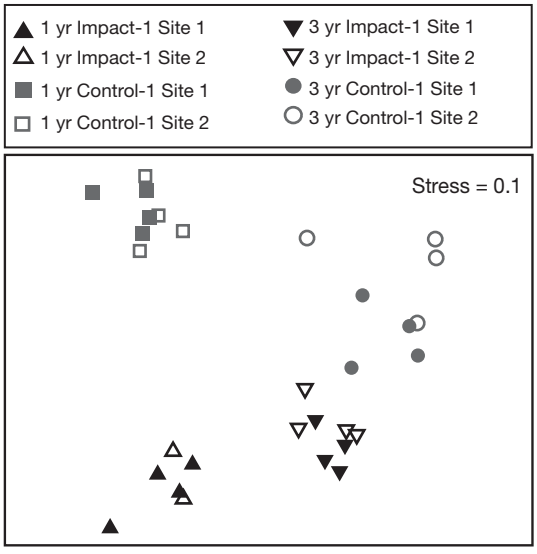

Fig. 6. nMDS scaling ordination of assemblages (combined upper and lower surfaces) on tiles at different sites (~50 m apart) at Impacted-1 and Control-1 at 1 and 3 yr

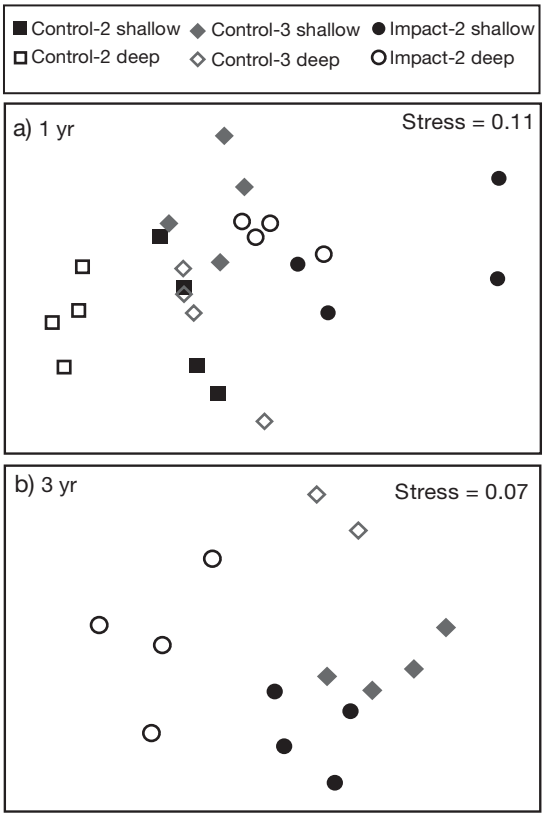

Fig. 7. nMDS ordination of assemblages (combined upper and lower surfaces) on tiles at shallow and deep sites at (a) 1 yr and (b) 3 yr

was tested (Impacted-1 and Control-1), there were no significant differences in assemblages between the 2 sites (~50 m apart) after 1 yr, but after 3 yr there was a small difference at Control-1 (Table 4, Fig. 6).

Human impacts

Impacted-1 (the waste disposal site) was the location that differed the most from other locations at both 1 and 3 yr (Table 3); it also differed significantly from the controls as a group (1 yr: R = 0.99, p = 0.001; 3 yr: R = 0.69, p = 0.001). It was also one of the least variable locations (Table 5). Impacted-2 (the sewage outfall) was the most similar to Impacted-1 after 1 yr and was significantly different from all controls (Table 3, Fig. 5), and the controls as a group (1 yr: R = 0.51, p = 0.001), although this also decreased by 3 yr (R = 0.41, p = 0.001). Impacted-2 was also the most variable location (Table 5). Impacted-1 and Impacted-2 are distinct from all other locations in the nMDS ordination for 1 and 3 yr (Fig. 5). There is some overlap of samples from Impacted-2 with those from control locations, but no overlap of Impacted-1 with controls. The impacted locations also changed the least from 1 to 3 yr (Fig. 5) and had the lowest ANOSIM R-values in the 1 and 3 yr comparisons (Impacted-1: R = 0.94, p = 0.001; Impacted-2: R = 0.91, p = 0.001). Control-3 showed the greatest change from 1 to 3 yr (Fig. 5, R = 1.0, p = 0.001).

Although there was very little recruitment and very few taxa on the upper surfaces of the tiles, SIMPER analysis indicated that the upper surfaces were important in contributing to differences between impacted

Table 3. Results of analysis of similarities (ANOSIM) tests comparing locations at 1 and 3 yr, showing R-value (with p-value). Significant results in **bold**; significance level adjusted using sequential Bonferroni procedure

	Impacted-1	Impacted-2	Control-1	Control-2
1 yr				
Impacted-2	**0.83 (0.001)**			
Control-1	**1 (0.002)**	**0.54 (0.001)**		
Control-2	**1 (0.002)**	**0.63 (0.001)**	0.06 (0.22)	
Control-3	**0.99 (0.003)**	**0.37 (0.001)**	0.15 (0.03)	0.21 (0.013)
3 yr				
Impacted-2	**0.89 (0.001)**			
Control-1	**0.71 (0.001)**	**0.62 (0.001)**		
Control-3	**0.98 (0.001)**	**0.43 (0.006)**	**0.47 (0.003)**	

Table 4. ANOSIM results for comparison of sites within locations. Significant results in **bold**, corrected for multiple comparisons

Site 1 vs. Site 2	R	p
1 yr Impacted-1	−0.11	0.53
1 yr Control-1	−0.16	0.86
3 yr Impacted-1	−0.08	0.63
3 yr Control-1	**0.43**	**0.03**

Table 5. PERMDISP2 multivariate analysis of mean distance from centroid and standard error for each location and time, in ascending order

	Average	SE
1 yr		
Control-1	12.23	1.49
Impacted-1 (waste site)	12.62	2.14
Control-3	13.49	3.22
Control-2	17.15	1.04
Impacted-2 (sewage)	18.18	3.13
3 yr		
Impacted-1 (waste site)	15.82	1.99
Control-1	18.81	2.17
Control-3	17.81	1.62
Impacted-2 (sewage)	19.40	1.97

and control locations. At 1 yr at Impacted-1 and Impacted-2, spirorbids on both surfaces and diatoms on the upper surface cumulatively accounted for 82 and 75%, respectively, to the total dissimilarity with the controls. After 3 yr, spirorbids were the only taxa on the upper surfaces that were still an important contributor to differences between control and impacted locations, although this contribution was much reduced. Taxa such as sponges and bryozoans on the lower surfaces were much more important in discriminating between controls and impacted locations at 3 yr.

Depth

At the locations where a depth comparison was possible (Impacted-2, Control-2 and Control-3), there were significant differences between assemblages recruiting to tiles at shallow and deep sites (Table 6, Fig. 7a) for all 3 locations at 1 yr and for Impacted-2 and Control-3 at 3 yr (Fig. 7b). SIMPER analysis indicated that sponge cover was greater at deep sites than shallow, and that spirorbids tended to have greater cover at shallow sites. Bryozoans were initially more abundant at deep sites at 1 yr (except for Control-3), but at 3 yr they were more abundant at shallow sites.

Table 6. ANOSIM results for tests of differences between depths at each location and time. All p-values represent best possible result for the number of permutations possible

	R	p
1 yr		
Control-2 shallow vs. deep	0.90	0.03
Control-3 shallow vs. deep	0.35	0.03
Impacted-2 shallow vs. deep	0.35	0.05
3 yr		
Control-3 shallow vs. deep	0.93	0.07
Impacted-2 shallow vs. deep	0.81	0.03

DISCUSSION

This study demonstrated that there are patterns in the recruitment and development of sessile epibiotic assemblages in Antarctica at higher taxonomic levels. A mix of classification levels was used, including functional taxonomic units (such as encrusting bryozoans), but even when the data was aggregated at the phylum level the patterns were very similar.

There was no pattern of spatial differences between controls after 1 yr, but by 3 yr assemblages recruiting to tiles showed clear differences between control locations, separated by several km. This comparison must be interpreted with some caution due to the absence of data from the third control location. Differences between controls at 3 yr were largely due to differences in the cover of various bryozoan groups, which probably reflect processes operating at small spatial scales, such as local differences in availability of recruits, or small-scale environmental differences, such as currents. Spatial variability in developing epibiotic assemblages is well-documented in non-polar regions, from scales of 10s of m to km (Keough 1983, Butler 1986, Glasby 1998). At Ryder Bay on the Antarctic Peninsula, colonisation and assemblage development at species level was highly site-specific and depth-dependant, but higher taxa patterns were not examined (Bowden et al. 2006). The level of variability within locations at Casey generally increased from 1 to 3 yr as the communities became larger (occupied more space) and more complex (more taxa). At the 2 sites where spatial variation at small scales was examined there were no differences between sites ~50 m apart at 1 yr, due to variation within sites at scales of 1 to 10 m, but by 3 yr there were small but significant differences within the control locations. The nMDS ordination of all locations, (Fig. 5) also illustrates the amount of variation that occurred between replicate samples within a location, and there was considerable spread of samples for some locations. This demonstrates the need for adequate spatial replication when comparing locations, with

replicates placed from 10 to 50 m apart to incorporate small-scale variability. Similar results were found by Glasby (1998) in a study of spatial variation in a temperate estuary, and other studies have also stressed the importance of capturing small-scale variation in larger-scale comparisons (Morrisey et al. 1992, Underwood 1993). While it is clear that there was small-scale variation within some locations in the present study, some of which may be attributed to depth effects, the most obvious pattern was the difference between control and impacted assemblages.

Human impacts

The impacted locations were significantly different from the control locations after 1 yr and while all locations were significantly different from each other after 3 yr, the impacted locations were still distinctly different from the control locations. The 2 differing types of impact also appear to have had different effects. These differences in assemblages may represent a response to anthropogenic disturbance that can be characterised at higher-taxon levels. Patterns of response to contamination at high taxonomic levels have been found in Antarctic soft-sediment assemblages (Lenihan et al. 2003), but hard substrata assemblages in Antarctica have not previously been examined in this way.

After 1 yr the upper surfaces of tiles adjacent to the waste disposal site at Brown Bay (Impacted-1) were very different from those at the control locations, with greater total cover, which consisted mainly of spirorbids, but with little to no diatom film, and these differences persisted after 3 yr. In contrast, the lower surfaces of tiles adjacent to the waste disposal site had the least cover of biota, almost no sponges and significantly less bryozoan cover than the controls, but the cover of spirorbids did not differ from the control locations. These assemblages also exhibited the least amount of change between 1 and 3 yr. The contaminants in Brown Bay are mainly metals from the waste disposal site, which leach into the bay during summer melt and are highly concentrated in sediments of the bay (Stark et al. 2003b). Bryozoans, in particular their larval stage, are sensitive to metals (Wisely & Blick 1967, Henry et al. 1989), with reduced survivorship of recruits after exposure to dissolved metals (Ng & Keough 2003). Temperate sponges are also sensitive to metals, which can affect their growth, fecundity and survival (Cebrian et al. 2003). Sponges filter large volumes of water and accumulate and exhibit toxic responses to metals (Patel et al. 1985, Hansen et al. 1995). In a survey of temperate bays contaminated by industrial pollution, very few species of sponges were found (Pansini & Pronzato 1975). This study provides preliminary evidence that metals in Brown Bay, either dissolved or in resuspended sediments, are affecting the recruitment and development of sponges and bryozoans.

Assemblages in Shannon Bay, the location of the sewage outfall, were more similar to the control locations than the waste disposal site, but there were some significant differences. The lower surfaces of tiles at Shannon Bay had the greatest total cover of biota, the greatest cover of spirorbid polychaetes (2 to 5 times that recorded at control locations) and sponges (at least twice that recorded at controls by 3 yr), but the least cover of bryozoans. In temperate ecosystems sponges have been found to be generally tolerant of sewage pollution; for example, Terlizzi et al. (2002) found that a sewage outfall did not affect the distribution of sponges, but affected the pattern of variability in the structure of sponge assemblages around the outfall site. Similarly, in this study, Shannon Bay had the greatest variability in assemblage structure and composition. In temperate marine bays heavily polluted by sewage, Pansini & Pronzato (1975) found rich assemblages of sponges and Muricy (1991) found that sewage did not affect the total percentage cover of sponges on vertical subtidal surfaces, though it did reduce the diversity and evenness of sponge assemblages. This study did not identify sponges to species, so it is not possible to determine whether sponge assemblages were less diverse at Shannon Bay, but the evidence suggests that the cover of sponges on tiles is greater in the presence of sewage. Sewage may be being directly utilised as a food source or it may indirectly affects sponges by influencing local primary production and increasing available food. This may also explain the increased cover of spirorbid polychaetes at the outfall site. Conversely, bryozoan cover was much lower than controls in a similar manner to the waste disposal site, suggesting that bryozoans are possibly intolerant of sewage or eutrophication in Antarctica. Alternatively, bryozoan recruitment at Shannon Bay may be inhibited by biological interactions, such as allelopathy (Davis et al. 1991, Dobretsov et al. 2004), although the low sponge and low bryozoan cover at Brown Bay does not support this hypothesis.

This study provides preliminary evidence that Antarctic bryozoans and sponges are sensitive to anthropogenic disturbance. Sponges appear tolerant of sewage and may even respond positively to eutrophication, while bryozoans appear sensitive to it. Sponges and bryozoans appear to be intolerant of contaminants from the waste disposal site, most of which are metals, but some of which are hydrocarbons (Stark et al. 2003b, 2005). Marine invertebrates exposed to stress (such as pollution) during their larval stage have

been shown to exhibit impaired performance in later life stages (Maldonado & Young 1999, Ng & Keough 2003). It is possible that larval/settlement-stage recruits are being affected by pollution at Casey, resulting in differences in recruitment and assemblage development. However, there remains a distinct requirement for ecotoxicological testing of these Antarctic taxa (Chapman & Riddle 2003). Some marine invertebrates, particularly annelids, are tolerant of some pollutants and even posses detoxification mechanisms, (e.g. Marcano et al. 1996), which, combined with opportunistic life history strategies (e.g. high fecundity, short generation time, year-round breeding, widespread dispersal), see them successfully inhabit contaminated areas. Spirorbids appear to be responding in an opportunistic manner to both disturbance types at Casey, as they were more abundant at disturbed locations on both upper and lower surfaces. On upper surfaces they were the main colonists, particularly at disturbed locations. There are tiles still in place at all locations at Casey, and it will be interesting to see whether these differences in assemblages are maintained in the long term.

The deployment of settlement panels in monitoring experiments appears to be a potentially useful method in Antarctica. Patterns of differences between control and impacted locations were clear, even with coarse taxonomic resolution. Coarse resolution in such monitoring situations allows for fast analysis times after tile collection and does not require expert taxonomic knowledge to identify to species level. However, further examination of species-level patterns would enable a better understanding of the processes influencing these assemblages. Other factors to consider when deploying settlement panels for monitoring in Antarctica include uniform depth, adequate small-scale spatial replication and analysis of both lower and upper surfaces. Ideally for monitoring they should be supplemented with other techniques to provide further information on ecosystem status, such as soft sediments.

Colonisation and succession patterns in Antarctica

This study demonstrated some clear patterns of epifaunal recruitment and assemblage development in Antarctica. Structurally, there was very little recruitment to upper surfaces and this seems to be a general pattern for Antarctica (Stanwell-Smith & Barnes 1997, Bowden et al. 2006). This may be a result of either pre-settlement preferences to lower surfaces, or post-settlement mortality of recruits on upper surfaces. Bowden (2005) found no evidence for settlement preferences in a study of recruitment at monthly intervals over 17 mo at Ryder Bay, Antarctic Peninsula, with comparable rates of recruitment on upper and lower surfaces and no species recruiting preferentially to upper or lower surfaces, other than algae. However, there were very different assemblages on upper and lower surfaces after 3 yr (Bowden et al. 2006), with similar patterns to those in the present study. Bowden (2005) suggested that these differences were most likely due to post-settlement mortality; however, plates were replaced monthly, which would limit any buildup of sediment on the upper surfaces. In this study there was significant accumulation of sediment on upper surfaces—between 12 ± 1.7% (mean ± SE) and 55 ± 8.2% cover. Thus, the presence of sediment may be influencing the settlement of larvae, with less available habitat (upper surfaces) and/or preferential habitat selection of sediment-free surfaces (lower surfaces). Alternatively, sediment deposition may cause post-settlement mortality via smothering. The effect of sedimentation on recruitment, however, has not been tested in Antarctica. In addition, the sediment on the upper surfaces was heavily colonised by tanaid crustaceans of the genus *Nototanais*, which are voracious predators of juvenile and small invertebrates (Oliver & Slattery 1985).

The general pattern of assemblage development and succession at Casey is of diatoms and spirorbids as pioneers on upper surfaces, with little development by 3 yr. On lower surfaces spirorbids and bryozoans were the pioneer colonists, and after 3 yr, spirorbids were still dominant but bryozoans occupied significantly more space and sponges also comprised a significant component of the assemblage.

This study reports some recruitment patterns that contrast with those found in other areas of Antarctica. Signy Island has very slow rates of colonisation on lower surfaces at 5 and 25 m depth, with <2 to 6% cover after 15 mo deployment and <9% after 21 mo (Stanwell-Smith & Barnes 1997). This may be a consistent pattern for Signy Island, as Barnes (1996) reported similar colonisation rates after 2 yr in an earlier study at the same location. At Ryder Bay the mean cover on lower surfaces after 3 yr ranged from ~25 to 68% at 8 m and ~6 to 70% at 20 m at 3 locations (Bowden et al. 2006). Mean colonisation rates at Casey are greater than other areas previously reported in Antarctica, with mean cover after 3 yr ranging from 81 to 91% at 3 control locations, with up to 98% mean cover at 7 to 10 m and 79 to 81% cover at 19 to 22 m. Some areas of Antarctica appear to be subject to considerable inter-annular variation in recruitment, possibly as a result of large-scale oceanographic variations. Settlement panels deployed at McMurdo Station in the 1970s had almost no recruitment after 5 yr, but 10 yr after deployment were described as 'well colonised' by bryozoans,

soft corals and sponges (Dayton 1989). The assemblage composition and structure at Casey is similar to both the Signy Island and Ryder Bay assemblages, with spirorbids and bryozoans dominant in all 3 regions. However, at Casey after 3 yr, sponges were a notable component of the assemblage (up to 17%), unlike the other 2 regions. Further evidence of regional differences comes from King George Island, where after 3 yr the substratum was almost entirely dominated by solitary ascidians (Rauschert 1991).

CONCLUSIONS

This study represents the first use of settlement panels in a monitoring context in Antarctica, which is a very difficult environment to work in, and where there is a real need for simple, robust techniques suited to a standardised monitoring procedure. It is also the first study of epibiotic colonisation from East Antarctica. Clearly there are significant regional differences in rates of colonisation and in assemblage structure in Antarctica. Some broadly separated regions appear to have similar dominant colonists (spirorbids and bryozoans) and colonisation rates, and thus the applicability of settlement panels for monitoring in other regions may be similar. Some tiles are still deployed at Casey and will be sampled in the future, when species-level analyses will also be done for the entire collection. Further work at the species level will enable the mechanisms and processes behind such patterns to be better understood, and will increase our understanding of anthropogenic impacts on Antarctic ecosystems.

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