

Marine colonization and biodiversity at Ascension Island and remote islands

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Little is known about colonization of remote island coasts by marine invertebrates, other than corals. The structure of hard substrata assemblages was investigated across Ascension Island's littoral zone in comparison with other sites. Arrays of acrylic panels were deployed at two sites for 2 years at Ascension Island to measure subtidal recruitment. Colonization of panels at Ascension I. was low, though space occupation, abundance and richness varied considerably. After ~1 and 2 years Ascension panels were <17 and <37% covered by fauna and each had <22 recruits and 54 recruits (per 100 cm²) respectively, amongst the lowest density of recruits reported. Recruitment rates of corals (25 m² year⁻¹) at Ascension I. were also similar to the lowest levels reported elsewhere (e.g. at Bermuda or Midway islands). Less dispersive animal types, e.g. cheilostome bryozoans, were poorly represented. Panels immersed in Tanzania and Scotland were >30% covered, with >76 recruits per 100 cm² and with bryozoans well represented after 1 year. Across-littoral surveys of established macrofauna at five remote islands (Ascension I., Easter I., Azores, South Georgia and Signy I., Antarctica) revealed similar trends of a rich sublittoral and lower littoral reducing drastically up-shore; molluscs dominating abundance and species numbers, whilst polychaetes, crustaceans and echinoderms were well represented. Established sessile animals occurred patchily at a mean density of 8.26 m⁻² but recruits had mortality levels >99%. Polar or remote temperate/tropical sites are typically less colonized than at non-remote, low latitudes but the lowest levels reported are at remote polar sites. Reduced colonization at Ascension island reflects remoteness.

Keywords: recruitment, isolation, dispersal, coral, latitude

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INTRODUCTION

Increasing isolation and decreasing size and age of islands all represent increasing challenges for coastal organisms to reach and establish on their shores. Ascension Island is a small, young (less than 1.5 million years old, see Mitchell-Thome, 1982) mid-ocean island 1500 km from the nearest (W African) continent margin. The native megafauna on this remote volcanic rock is famously dominated by geographid land crabs, seabirds and green turtle migrants. The littoral and sublittoral fauna have been little studied and its shores appear quite barren (partly attributed to trigger fish grazing, see Price & John, 1978, 1980), though it is known to include many endemics. Numerous coastal amphipods, more than 15% of its shore fish, two shrimps (*Procaris ascensionis* Chace & Manning 1972 and *Typhlatya rogersi* Chace & Manning, 1972) and other invertebrates have been found nowhere else (Lubbock, 1980; Biernbaum, 1996). Remote Atlantic islands have been important for studies of terrestrial organism colonization and dispersal, but such places also represent equally good opportunities to examine marine colonization. Holmes *et al.* (1997) used artificial substrata (settlement panels) in the west Pacific to show that sublittoral colonization was lower on offshore than nearshore islands, mainly due to the rarity of taxa with non-planktotrophic

larvae, such as most cheilostomatid bryozoans. However, cheilostomatid bryozoans were major colonizers of panels deployed at old, remote islands, such as Signy I., Antarctica and arctic Spitsbergen (Stanwell-Smith & Barnes, 1997; Barnes & Kuklinski, 2005). These authors were unclear though, whether the low colonization was attributable to their locations being polar or isolated. Ascension I. is an ideal study site for investigation of how dispersal opportunities of a taxon influences representation at 'hard targets' such as remote, young islands. Examining levels of colonization at Ascension I. should aid interpretation of results from colonization studies of isolated localities elsewhere.

When Barnes (1996) and Stanwell-Smith & Barnes (1997) reported very low overall levels of space occupation on settlement panels immersed at Signy I. Antarctica, they suggested that polar colonization rates were very low. A new study of recruitment to immersed coastal panels in arctic Spitsbergen also found very little fauna compared with typically reported levels of richness, space occupation or abundance (Barnes & Kuklinski, 2005). Although old, the islands of Signy and Spitsbergen are both situated in mid-ocean archipelagos, so remoteness is also a potential explanation for reduced metrics of colonization compared with elsewhere. Recent studies of recruitment to subtidal settlement panels around the continent margin of Antarctica have revealed much higher levels of colonization, as well as high between-site variability (Bowden *et al.*, 2006; Stark unpublished data). Both Bowden *et al.* and Stark's studies showed levels of colonization after 2–3 years that fall within the variability reported from equivalent temperate and tropical experiments (Winston & Jackson, 1984; Todd, 1998;

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Maughan, 2000). Holmes *et al.* (1997) found the effect of isolation was much greater than latitude in the colonization of subtidal panels along the east Australian coast and similarly Davenport & Stevenson (1998) found impoverished littoral colonization at remote South Georgia compared with nearshore Cumbrae I. In contrast Schoener *et al.* (1978) found colonization of panels submerged at isolated Hawaii to be similar to patterns in Thailand. Comparisons are difficult as there are so few data reported from remote localities, with the possible exception of coral recruitment. Surveys of faunistic richness or diversity of adult communities have been reported for some remote island coasts (e.g. Węsławski *et al.*, 1988; Beckley & Branch, 1992; Cole *et al.*, 1992; Bourmaud *et al.*, 2005) but more typically such studies are restricted to one zone or group of animals (e.g. Moyano, 1973; Pugh & Mercer, 2001; Bouchet *et al.*, 2002). Coral recruitment has been the major focus of investigations into marine colonization of remote islands, such as at Hawaii and Bermuda (see Fitzhardinge, 1985; Smith, 1985, 1992; Friedlander *et al.*, 2005). Few studies have ever reported rates across marine fauna for a remote tropical (or temperate) island.

In the current study the biodiversity of isolated localities (focusing on Ascension I.) was investigated using artificial substrata and surveys from the subtidal to the supralittoral. Acrylic settlement panels were deployed in the shallow subtidal for 2 years at Ascension I. and, for comparison, at two continent margin sites – a matched tropical latitude in Tanzania and a temperate site in west Scotland (UK). Surveys of sublittoral, littoral and supralittoral macrobenthos were conducted at Ascension I., Easter I., the Azores, and South Georgia and Signy islands in Antarctica. The aim of the current study is to determine the rates and variability of coastal colonization at an isolated young tropical locality and its pattern of richness across the terrestrial-marine interface zone. It is hypothesized that at Ascension I.: (1) colonization to panels will be low and that taxa with non-pelagic larvae will be poorly represented; and (2) trends of richness from sublittoral to supralittoral zones will show similar patterns to elsewhere but with overall depressed levels.

MATERIALS AND METHODS

Young and established coastal communities at Ascension I. (South Atlantic) were investigated using settlement panels to measure recruitment and transect surveys to quantify established adults. Recruitment was measured at two other non-remote sites and adult communities were assessed at several other remote sites for comparison with Ascension I. data.

Study apparatus and area

Artificial substrata in the form of settlement panels ($15 \times 15 \times 0.5 \text{ cm}^3$) were deployed in the shallow subtidal zone at a series of sites. Each panel was cut from black acrylic sheet and machine-sanded (following Turner & Todd, 1993; Todd & Keough, 1994; Barnes & Kuklinski, 2005; Bowden *et al.*, 2006). A central ($10 \times 10 \text{ cm}^2$) analysis area was marked out by drilling a 0.1 cm groove. Panels were attached to two Perspex rods in threes using plastic nuts and bolts (of 0.5 cm diameter). Panels were then washed and conditioned (to develop a biofilm) by immersion in local seawater for a period of 3 days. The approximate location for placement of each panel array was selected at random but within these locations, areas were selected which were most sheltered from wave action to minimize chances of dislodgement or damage. Small stainless steel (316 marine grade) hoops were attached to rock surfaces using two-part aquarium cement and left for 2 days to harden. Each conditioned triplicate array was then attached, using cable ties, to these stainless steel hoops. Arrays were mounted such that each was approximately horizontal and plastic spacers were used to ensure the under-surface of each panel was $\sim 2 \text{ cm}$ above the substratum.

At Ascension I., two sites ($\sim 100 \text{ m}$ apart) were selected for panel deployment at each of two localities ($\sim 5 \text{ km}$ apart), English Bay and North East Bay (see Figure 1). Investigation of established adult communities also encompassed a further locality of Shelly Bay. The main difference between these sites was exposure to wave action and prevailing wind.

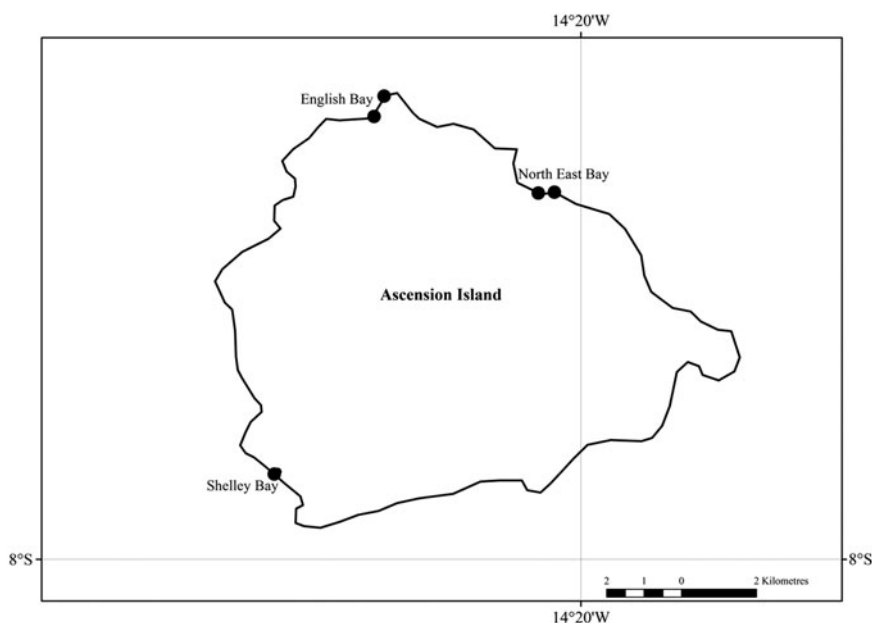


Fig. 1. Position of study sites (filled circles) at Ascension Island, mid Atlantic.

Shelly Bay was the most exposed to wind and wave and accumulated large amounts of floating volcanic rock (pumice) and other marine debris on the shore. North East Bay was mainly affected by ocean swell and English Bay was the most sheltered, but all three localities would be considered very exposed compared with most European shores (approximate to Ballantine 2–3 sensu Ballantine (1961)). The 24 panels deployed encompassed variability across the scales of km, 100 m, and replicates by this experimental design. Three areas of similar size to panels were scrubbed clean of encrusting biota at each of the two locations. The two bays were characterized by high wave energy, low tidal ranges (~ 1.3 m) and volcanic bedrock with few boulders. Little is known of the ecology of coastal marine invertebrates at Ascension I. (but see Irving, 1989) though a number of studies have attempted to describe the species of specific taxa (see Maddocks, 1975; Rosewater, 1975; Markham, 1978; Pawson, 1978; Manning & Chace, 1990; Biernbaum, 1996; Hoeksema *et al.*, 2017; Zibrowius *et al.*, 2017). During the same study period as the panel deployments at Ascension I., identical panel arrays were also deployed at two localities at each of the following locations; Oban in West Scotland (UK) and the east coast of Pemba I., Tanzania. Comparisons were also made with settlement panel studies using similar apparatus and protocol during the same time period in west Spitsbergen (Svalbard Archipelago, Arctic Norway) (Barnes & Kuklinski, 2005), Lough Hyne, South West Ireland (Watson & Barnes, 2004) and Adelaide I., Antarctica (Bowden *et al.*, 2006). The location of the main study areas and important areas of comparison are shown in Figure 2.

Protocol

Panel arrays were deployed across the years 2002 and 2003. Panels were resurveyed after 1, 3, 11 and 24 months immersion at Ascension I.; 3, 6, 12 and 24 months in W Scotland and 3, 4, 7, 8 and 13 months in Tanzania. A first deployment

of panels to the intertidal and shallow subtidal zones at Ascension I. resulted in most panels being lost to storm damage and a series of panels experimentally deployed at 6 m depth were all carried away by wave action. New deployment using more aquarium cement around the stainless steel hoops and more sheltered microhabitats proved more successful. On retrieval all panels were photographed using a digital camera (Nikon D100 fitted with microNikkor 60 mm macro lens in an underwater housing) and stored as high-resolution jpg files (with zero compression). Panels were then replaced in the same positions and reattached using new cable ties. Each individual recruit in the central analysis area of each panel was counted (each colony was recorded as one recruit) and identified to the lowest possible taxonomic level using primary literature. The degree of space occupation (% cover) was evaluated using image analysis, and the number of recruits, genera and classes of animals were counted and recorded per panel. The data were analysed using General Linear Model (GLM) ANOVA in the software package MINITAB 14. The dependent variables were successively percentage cover, generic richness, class richness and density (number of individuals m^{-2}). The independent factors at each were spatial (locality and site) and time (duration of immersion). Per cent cover values were arcsine transformed and then all data were checked for normality and homogeneity of variance prior to ANOVA (GLM).

The richness of fauna was investigated along transects at three localities at Ascension Island: English Bay, North East Bay and Shelley Bay. Each transect was sampled at 6 and 3 m below Extreme Low Water Spring tide level (ELWS), Lower, middle and upper shore and 3 and 6 m above Extreme High Water Spring tide level (EHWS). On each transect at each of these heights five 1×1 m² quadrats were randomly deployed, the fauna within them examined and all macroscopic (>3 mm) animals identified and counted. A similar protocol was carried out adjacent to the towns of Ponta Delgada, Sao Miguel I. (Azores Archipelago) in 1998,

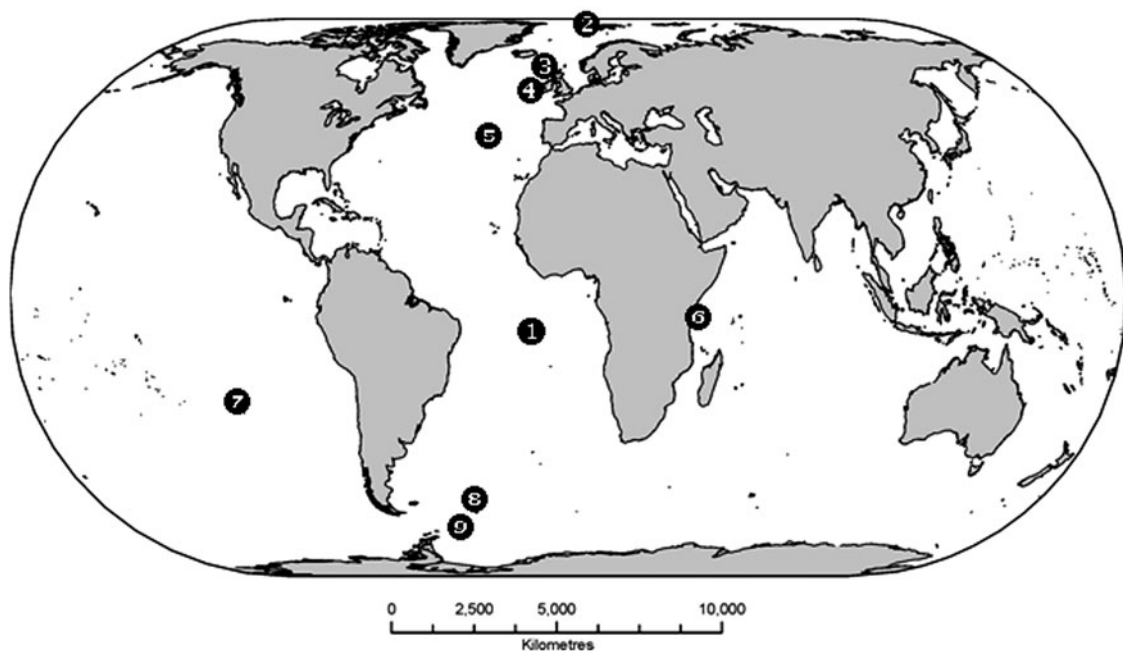


Fig. 2. Sites of coastal colonization and richness studies. The sites are Ascension Island (1), Spitsbergen Island, Arctic (2), W Scotland (3), SW Ireland (4), Miguel Island, Azores (5), Pemba Island, Tanzania (6), Easter Island (7), South Georgia (8) and Signy Island, Antarctica (9).

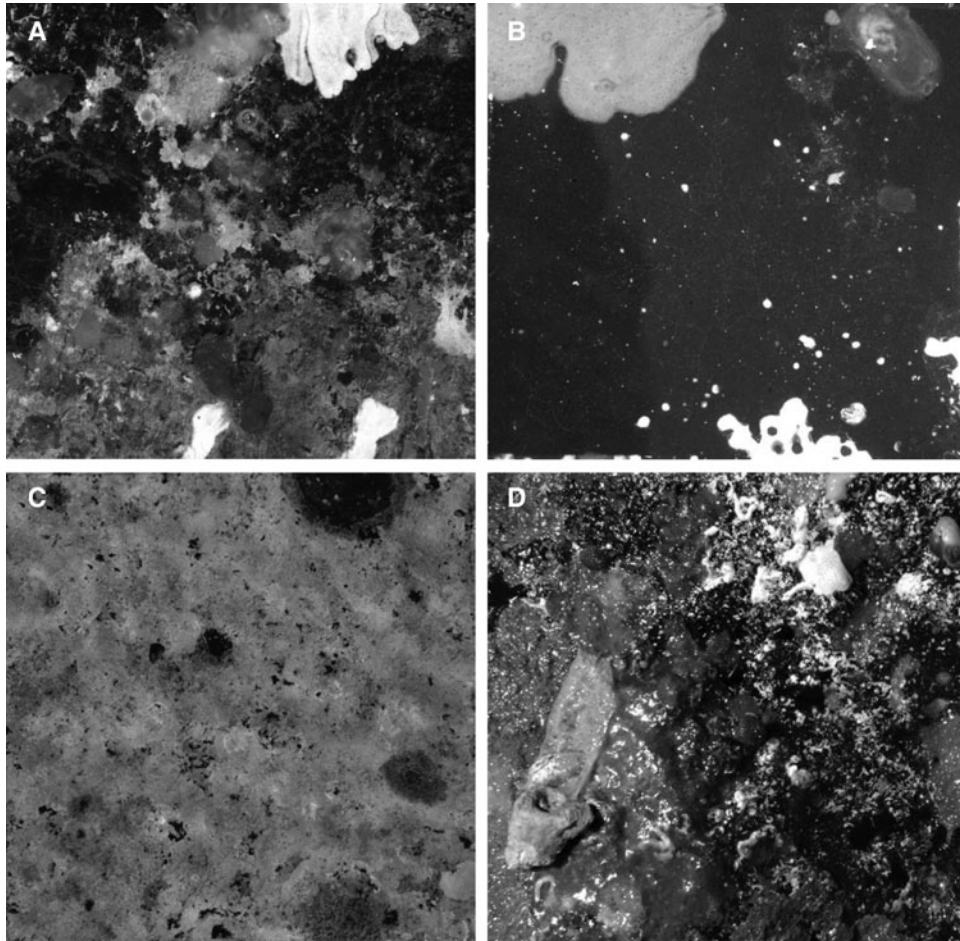


Plate 1. Variability in the level of space occupation and composition of colonizers on settlement panels at Ascension Island. (A and B) are from English Bay, (C) is from North East Bay and D is recolonization of natural rock at North East Bay.

Hanga Roa, Easter I. (Mid Pacific) in 2002 and in Cumberland East Bay, South Georgia in 2005 and Borge Bay, Signy Island (Antarctica) in 1993. Data were displayed as scatter plots of (mean and total) numbers of species with height across the nearshore terrestrial, intertidal and shallow subtidal zones.

RESULTS

During the course of the study four of the 24 shallow subtidal panel arrays were destroyed at Ascension I. The first settlers on the panels were polychaete (serpulid and spirorbid) worms and solitary ascidians but eventually were also colonized by anthozoan and hydrozoan cnidarians, bivalve molluscs, cheilostome bryozoans and demosponge Porifera. At 11 months the major space occupiers were demosponges and colonial ascidians (Plate 1) and after 2 years the panels had developed an encrusting biota that was similar to assemblages on surrounding large boulders. ANOVA identified neither locality nor site as significant factors influencing variability in (genus or class level) richness, abundance or space occupation of assemblages recruiting to the panels at Ascension Island (All ANOVA, $F_{1, 1} < 0.94$, $P > 0.34$). The space occupied by encrusting fauna reached a mean of ~36% by 2 years, though this varied considerably between panels (12.6–72.4% – Figure 3A). Both the numbers of genera and classes of recruits increased rapidly at first but

then little from 11 to 24 months, finishing at means of 5.67 and 7.35 for these durations (Figure 3B). Recruit abundance was very low and, especially by the end of year 2, was highly variable with a mean of 54 recruits per panel (per 100 cm²) established by the end of the experiment. Coral recruitment was highly variable both on the artificial panels (mean: 0.25 per panel/25 per m²) and adjacent rock surfaces (0–29 m²) experimentally cleared for comparisons.

The space occupation by encrusting fauna on panels was significantly different across regions (Table 1). Percentage cover at Pemba I, Tanzania and W Scotland were considerably higher than at Ascension I. (Figure 4A). There was little difference in space occupied after the first few months between panels at Ascension I. and other study regions. However, by the time panels had been immersed for about 1 year, fauna, including a diversity of cheilostomatid bryozoans, had covered 35.6% (± 3.3) of panels in Tanzania and 30.0% (± 2.9) of those in W Scotland compared with <20% at Ascension I. (Figure 4A). Recruitment to the Tanzanian panels was, at 76.8 per 100 cm² (mean total) and 0.33 per 100 cm² (coral), more than double that observed at Ascension I. over a similar period but represents less than half the number recruited to the Scottish panels after 12 months (Figure 4B).

Much of the fauna in the sublittoral, littoral and supralittoral at Ascension I. was cryptic, occurring under boulders or in crevices, resulting in all zones having a denuded appearance.

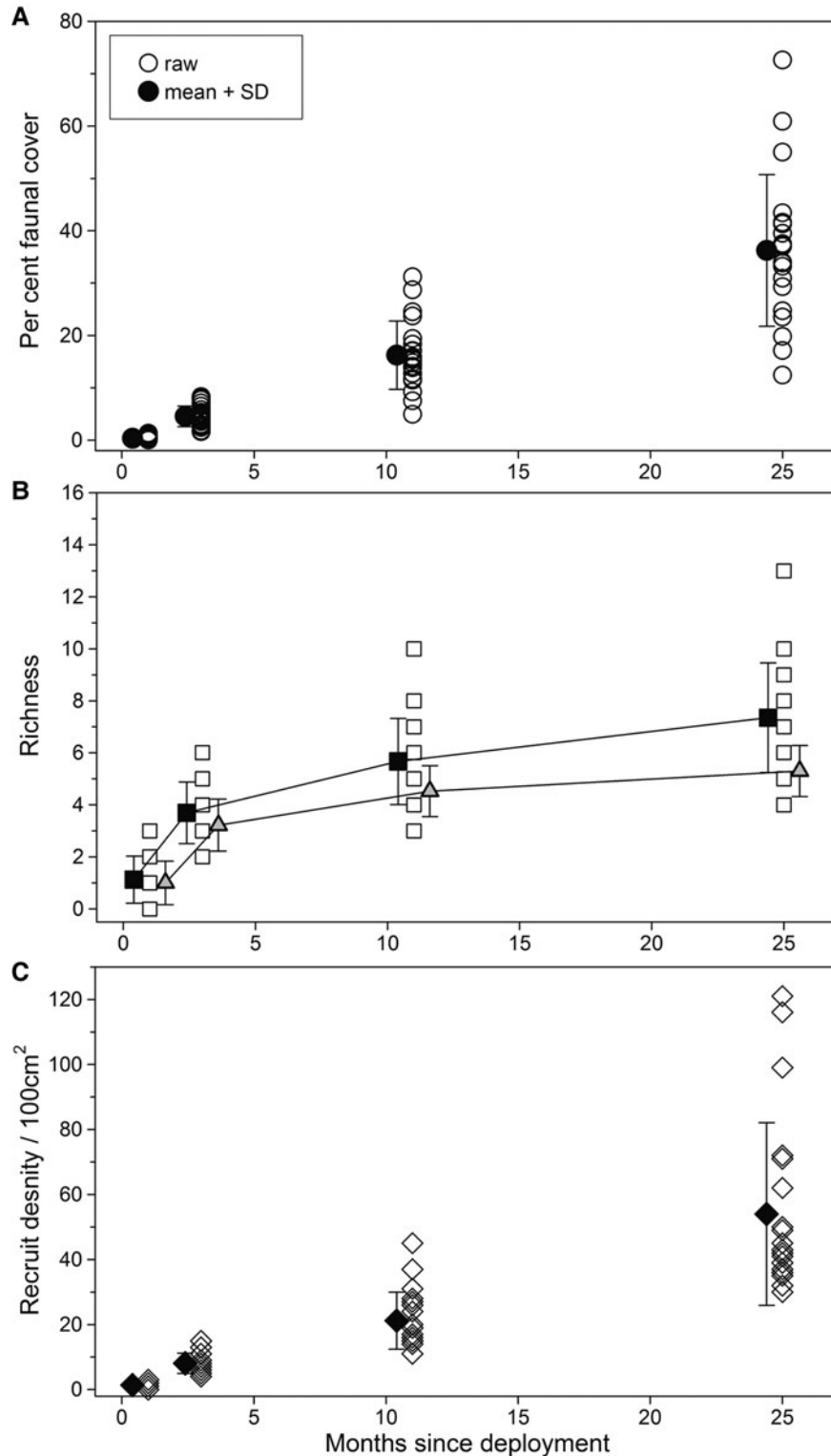


Fig. 3. Space occupation (a), richness (b) and recruit density (c) on shallow subtidal settlement panels at Ascension Island with time. The raw data are offset (on the x axis) from mean values for clarity.

Molluscs (49.5%) and polychaete worms (15.8%) dominated littoral numerical abundance though casual observation suggested echinoderms would dominate the biomass. A total of 35 macrofaunal, principally (endemic) mollusc and crustacean species, were identified along the three Ascension I. subtidal-supralittoral transects (Table 2). The pattern of mean and

total species richness was similar across all three Ascension I. study localities (Figure 5), being high in the subtidal and lower shore but drastically declined (<50% species) on the mid-shore. Macro-fauna were observed in pools with water temperatures of up to 41°C, though few macro- or mega-faunal species were obvious above the upper shore, where (colonized)

Table 1. ANOVA of region (Ascension Island, Tanzania and Scotland), duration of panel immersion and locality.

Source	df	Seq SS	Adj SS	Adj MS	F	P
Region	2	2827.8	1355.8	677.9	12.5	<0.001
Time	1	25354.6	25057.8	25057.8	463.5	<0.001
Locality	3	251.7	251.7	83.9	1.6	0.204
Error	135	7298.0	7298.0			
Total	141	35732.1				

rock temperatures exceeded 56°C. Transect and quadrat surveys, using the same method and apparatus, of macro- and mega-fauna across the littoral zone of other remote islands revealed similar patterns (Figure 6). Richness at subtropical Easter Island and Sao Miguel, Azores both showed increased variability overall and more species (and individuals) in the supralittoral compared with Ascension Island. Across the littoral and supralittoral zones the mean richness of species at the Antarctic localities, Signy Island and South Georgia, were similar to that at Ascension I. (though the variability differed considerably).

Adult sessile fauna formed $69 \pm 3.2\%$ of established individuals and $55.9 \pm 3.2\%$ of species recorded in the shallow

subtidal of Ascension I. The high level of standard deviation associated with density, $8.26 \pm 7.3 \text{ m}^2$, indicates pronounced patchiness associated with a high (5400–8.26 adults $\text{m}^2 = 99.84\%$) post-settlement mortality. Brief observations revealed that this mortality was associated with wave action moving boulders and transient fishes.

DISCUSSION

Colonization of the Ascension Island coast by marine invertebrates was highly variable in scale comprising types of organism which typically recruit to hard substratum elsewhere. The mean rate of colonization of panels deployed in the shallow subtidal was found to be very low (Figure 3), but general levels of recruitment are, however, consistent with the few studies reported from other remote islands (Table 3). The richness and patterns in richness of established (adult) communities across the littoral zone were approximately similar to those on the other studied mid-ocean islands across latitude (Figure 6). Comparing the natural density of recruits to established adults on the panels indicates a massive post settlement mortality.

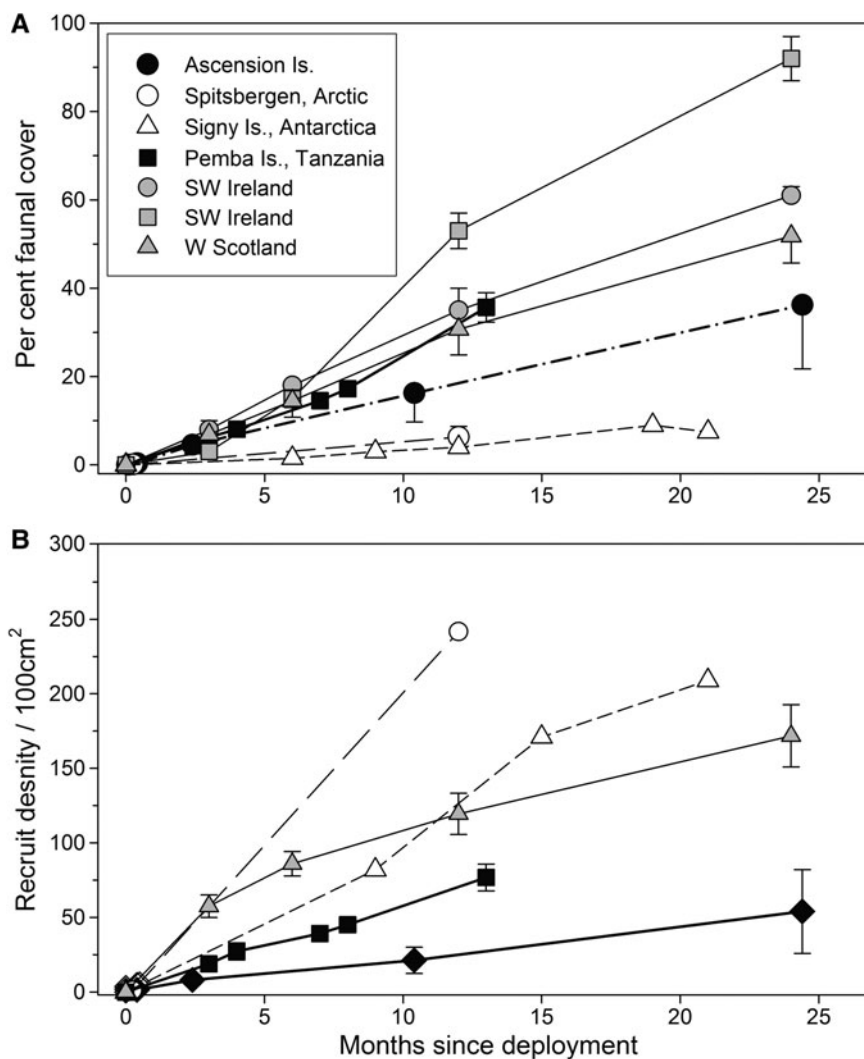


Fig. 4. Mean space occupation (a) and recruit density (b) on shallow subtidal settlement panels with time and location. The key to locations is shown in (A). Data for Spitsbergen are from Barnes & Kuklinski (2005), for Signy Island from Stanwell-Smith & Barnes (1997) and for SW Ireland from Maughan (2000).

Table 2. Macro/megafauna present in study quadrats from 6 m below Extreme Low Water Spring tide level to 6 m above Extreme High Water Spring tide level at three sites on Ascension Island.

Taxa	English Bay	Mars Bay	NE Bay
Annelida			
<i>Eurothoe complanata</i> Pallas 1766			✓
<i>Hermodice carunculata</i> Pallas 1766	✓		
<i>Pileolaria</i> sp.	✓		✓
Serpulidae	✓		✓
Crustacea			
<i>Alpheus macrocheles</i> Hailstone 1835		✓	
<i>Calcinus tubularis</i> (Linnaeus 1767)	✓		✓
<i>Clibanarius tricolor</i> (Gibbes 1850)			✓
<i>Cronius rubber</i> (Lamarck 1818)			✓
<i>Johngarthia lagostoma</i> (H Milne Edwards 1837)	✓	✓	✓
<i>Grapsus adscensionis</i> (Osbeck 1765)	✓	✓	✓
<i>Paractaea rufopunctata</i> (H Milne Edwards 1834)		✓	
Unknown amphipod	✓		
Echinodermata			
<i>Diadema antillarum</i> Philippi 1845	✓	✓	
<i>Echinometra lucunter</i> (Linnaeus 1758)	✓	✓	✓
<i>Eucidaris clavata</i> Mortensen 1928	✓		✓
<i>Ophiactis savignyi</i> (Müller & Troschel, 1842)		✓	✓
Mollusca			
<i>Arca noae</i> Linnaeus 1758			✓
<i>Cypraea lurida</i> (Linnaeus 1758)		✓	✓
<i>Fissurella nubecula</i> (Linnaeus 1758)			✓
<i>Mitra barbadensis</i> (Gmelin, 1791)		✓	
<i>Mitrella ocellata</i> (Gmelin, 1791)	✓		✓
<i>Nassarius</i> sp.	✓		
<i>Nerita ascensionis</i> (Gmelin, 1791)		✓	✓
<i>Echinolittorina miliaris</i> (Quoy & Gaimard, 1833)	✓	✓	✓
<i>Octopus vulgaris</i> Cuvier 1797	✓		
<i>Saccostrea cucullata</i> (Born 1778)	✓	✓	✓
<i>Stramonita rustica</i> Lamarck 1822	✓	✓	✓
<i>Platydoris</i> cf. <i>angustipes</i> Morch 1863	✓		
Cnidaria			
<i>Favia gravida</i> Verrill 1868		✓	
<i>Millepora</i> sp.	✓		✓
<i>Medracis</i> sp.	✓	✓	
<i>Siderastrea radians</i> (Pallas, 1766)	✓	✓	✓
Porifera			
<i>Haliclona</i> sp.	✓		✓
<i>Crambe</i> sp.	✓	✓	✓
Unknown demosponge 1	✓	✓	
Unknown demosponge 2		✓	✓
Unknown demosponge 3			✓
Bryozoa	✓		✓
Terrestrial insects	✓	✓	✓

Colonization of artificial substrata

Taxa with planktonic wide-dispersing larvae, particularly small tubicolous polychaete worms (spirorbidae) and ascidians, were the earliest recruiting taxa and were the initial major space users on subtidal panels at Ascension I. This appears typical for recruitment onto shallow hard surfaces for localities reported worldwide (Goren, 1979; Lopez Gappa, 1989; Rauschert, 1991; Dalby & Young, 1992; Relini

et al., 1993; Maughan, 2000; Barnes & Kuklinski, 2005). Despite, as reported elsewhere, considerable variability in colonization levels between panels, variability between sites within Ascension I. was not significant and in terms of space covered after a few months, colonization rates at Ascension I. were similar to those of the continental margin at both Tanzania and W Scotland as well as other values reported from low latitudes (Figure 4A). However, many low latitude studies have reported much higher coverage (>50%) after just a few months' immersion (e.g. Jackson, 1977; Schoener & Schoener, 1981; Barkai & Branch, 1988; Maughan, 2000; Glassom *et al.*, 2004). Ascension I. faunal cover was, after nearly 1 year of immersion (mean 16.2%), considerably lower than reported from most temperate and tropical sites. In the north Atlantic Maughan (2000) reported that panels immersed for a year, across a variety of depths and flow rates, were nearly completely covered by fauna while Caribbean panels immersed for similar periods can be nearly 90% covered (e.g. Winston & Jackson, 1982; Carlon, 2001). However Arnold (2011) found cover as low as 24% and 28% after a year in Guatemala and Belize respectively (rising to 51% and 43–60% by year 2). Coverage of Ascension I. panels was more comparable with some remote or polar sites (Holmes *et al.*, 1997; Bowden *et al.*, 2006) but higher than that reported from remote (and) polar sites (Barnes, 1996; Barnes & Kuklinski, 2005). Despite there clearly being many spatial, temporal and other (such as flow rate or predation) factors causing considerable intra-site variability, it seems that typically rate of space occupation can be ranked as temperate/tropical > polar and remote temperate/tropical > remote polar. Geological age is likely to be superimposed over such ranking with older islands having much richer and diverse marine assemblages.

The number of taxa (genera) present on panels immersed at Ascension I. was similar to two sites at Hawaii after the same period (Schoener *et al.*, 1978). Richness between panels varied by a factor of three, but was not linked to site. As with space occupation though, taxon accumulation overall was considerably lower than reported from most temperate and tropical studies of non-remote sites (e.g. Jackson, 1977; Goren, 1979; Schoener & Schoener, 1981; Field, 1982; Pisano & Boyer, 1985; Holmes *et al.*, 1997). The hypothesis that richness levels would be low at isolated Ascension I. compared with reported rates of taxon accumulation onto similar panels at non-remote localities can be accepted. Also, as hypothesized, few (only three) cheilostomatid bryozoan morpho-types (identity not resolved in the current study) were found. Holmes *et al.* (1997) also found few bryozoans on their offshore sites, even though these were much closer to the continental shelf than Ascension I. The scarcity of different bryozoans on panels at Ascension I. contrasts strongly with reported richness in early assemblage development on panels elsewhere. The essentially benthic, lecithotrophic larvae typical of most cheilostomatid bryozoans, have much reduced dispersal opportunities compared with those of the main colonizing taxa (spirorbid and serpulid polychaetes, demosponges, ascidians and barnacles) at Ascension I. and elsewhere, which have mainly pelagic larvae (of various durations). Bryozoans seem to be poorly represented at young (Arntz *et al.*, 2006) but not old isolated polar islands (Stanwell-Smith & Barnes, 1997; Barnes & Kuklinski, 2005), though no actual panel or other colonization studies have been reported from a young remote polar island to date.

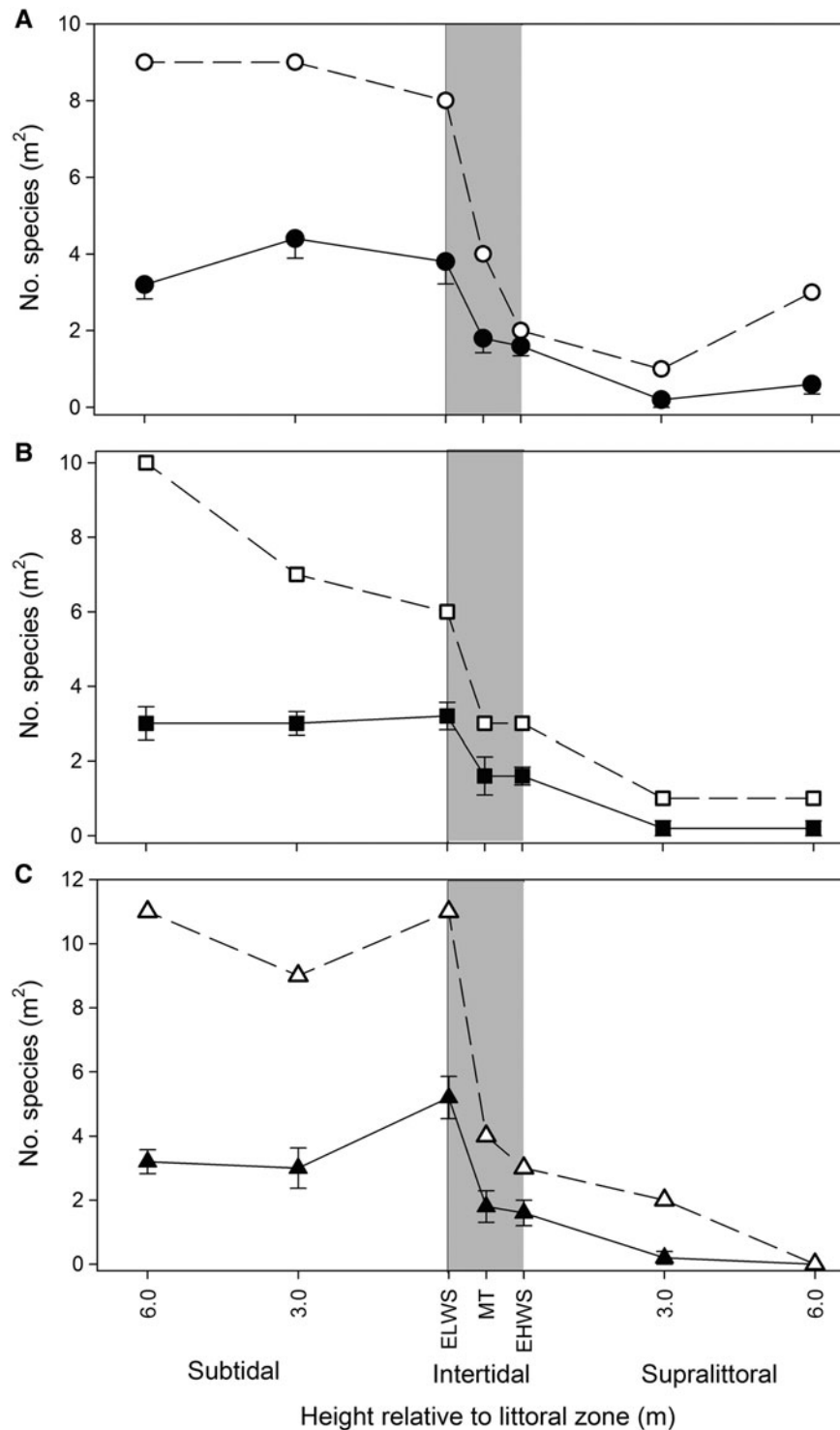


Fig. 5. Total (open symbols) and mean numbers (filled symbols) of established macro-epifaunal species across the land–sea interface zones at three sites at Ascension Island. The three sites are English Bay (a), North East Bay (b) and Shelley Bay (c). The littoral zone is shaded in grey and means are shown with standard error. ELWS, Extreme Low Water Spring tide level; EHWS, Extreme High Water Spring tide level; MT, Mid tide level.

Recruit abundance or density has been one of the most measured metrics of marine colonization to panels or natural substrata. At Ascension I. overall recruit densities were very low, lower than at other tropical, temperate or polar sites reported in the literature (Figure 4B) (e.g. Goren, 1979; Chalmer, 1982; Pisano & Boyer, 1985; Todd, 1998; Maughan, 2000). Even some studies of single taxa, such as corals or barnacles, recruiting to panels have recorded

higher densities (Fisk & Harriott, 1990). Most studies on hard-substratum recruitment of tropical and subtropical shores have focused on the hermatypic corals.

Coral recruitment

In the last two decades a large literature has developed on the spatial and temporal variability of coral recruitment rates.

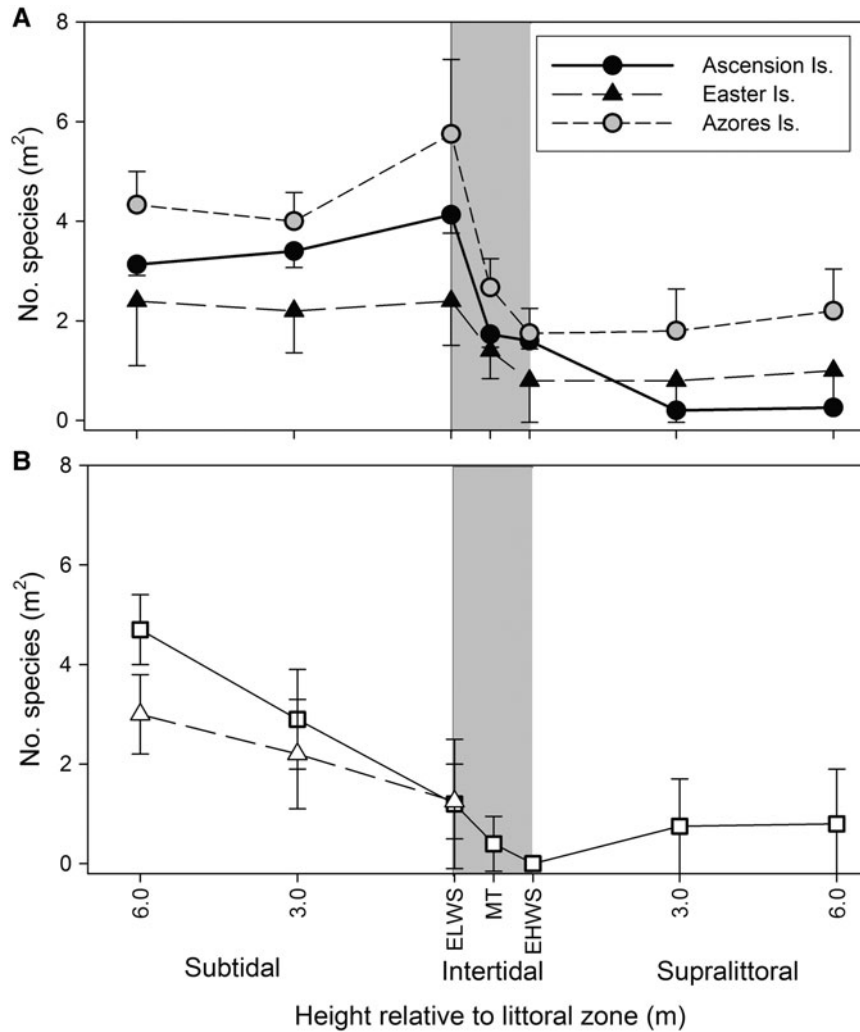


Fig. 6. Mean numbers of established macro-epifaunal species across the land–sea interface zones at three sites at three low (upper plot) and two high (lower plot) latitude mid-ocean islands.

This includes studies from continent margins to offshore islands and even a few mid ocean islands. The current study value of 25 m^{-2} at Ascension I. is comparable with the lowest levels found elsewhere at Atlantic locations (Table 4), except at Guatemala where Arnold (2011) recorded virtually no recruitment over two years. Ascension I. recruitment levels were similar to those reported from the other remote Atlantic island studied (Bermuda, see Smith 1985, 1992). Coral recruitment to panels and adjacent natural substrata at Ascension I. were comparable, but were low. Smith (1992) found lower levels of coral recruitment to panels in Bermuda, but this was confounded by panel and natural

substratum data being collected in different years. Most of the highest coral recruitment levels (to natural reefs rather than settlement panels) in the Atlantic have been reported from Curacao, but these have declined from 15.3 per m^2 in 1976 to 6.9 per m^2 by 2005 (Vermeij *et al.* 2011). Values from Pacific localities vary more than those reported from the Atlantic but are typically higher (Table 4). Nevertheless the coral recruitment measured from 2003 to 2005 at Ascension I. was higher than measured during a similar time period at the remote Pacific (Hawaiian) islands of Midway (7 m^{-2}) and Pearl and Hermes (18 m^{-2}) (Friedlander *et al.*, 2005). Friedlander *et al.* (2005) reported

Table 3. Previous recruitment studies using settlement panels in the subtidal zone at remote islands.

Location	Latitude	% Cover	Classes/species	Duration	Depth (m)	Panel size (cm)	Authors
Spitsbergen	78°N	3–11	3/20	1 years	12	15 × 15	Barnes & Kuklinski (2005)
Bermuda	36°N	ND	Corals	4–9 months	5–7		Smith (1985)
NW Hawaii	25°N	ND	Corals	~4 years	20	15 × 15	Friedlander <i>et al.</i> (2005)
Hawaii	21°N	ND	5/8	1 years	16	15 × 31	Schoener <i>et al.</i> (1978)
Lord Howe I.	31°S	1–4	1/20	1.3 years*	6–9	15 × 15	Holmes <i>et al.</i> (1997)
Signy I., Ant	60.5°S	0.1–3	3/22	~2 years	6, 12, 25	15 × 15	Barnes (1996)
Signy, Ant	60.5°S	2–10	4/23	~2 years	5, 8, 25	15 × 15	Stanwell-Smith & Barnes (1997)

Table 4. Coral recruitment onto settlement panels with location and experiment duration.

Location	Coral recruits (m ⁻² yr ⁻¹)	Duration months	Authors
Ascension I.	25	24	This study
Bermuda	15–160	2–9	Smith (1985, 1992)
Florida	130–270	ND	Smith (1997)
St Croix	80–90	26	Rogers <i>et al.</i> (1984)
Jamaica	8–370	11	Sammarco (1980)
British Virgin Islands	133–333	24	Carlson (2001)
Mexico	123	18	Baggett & Bright (1985)
Red Sea	190	3–4	Glassom <i>et al.</i> (2004)
Tanzania	1–21 33	24	Nzali <i>et al.</i> (1998), This study
Komodo, Indonesia	285–772	36	Fox (2004)
Great Barrier Reef	22–879	12 6	Wallace (1985), Fisk & Harriott (1990)
Lord Howe I.	0.1–1.1%	4–8	Holmes <i>et al.</i> (1997)
Guam	160	6	Birkeland <i>et al.</i> (1981)
Hawaiian archipelago	2–230 7–270	6 60	Fitzhardinge (1985), Friedlander <i>et al.</i> (2005)
Tahiti	131	4	Gleason (1996)

coral recruitment levels at least an order of magnitude higher at other Hawaiian islands, levels which seemed to be little different from non-remote localities such as the Great Barrier Reef, Australia. The most recent review of coral recruitment at Ascension Island is that by Irving (2013). Current study values from Tanzania are little different to those reported from other protected areas in the region (Nzali *et al.*, 1998), or indeed from levels at Ascension Island. The level of cover by corals was very low and may help to explain the low recruitment found on panels. Direct relationships between adult coral cover and larval recruitment are debated (Nzali *et al.*, 1998; Hughes *et al.*, 2000).

Mortality and links between recruitment and establishment

Price & John (1978, 1980) suggested trigger fish (*Melichthys niger*) to be important agents of mortality to Ascension I. benthos. They also reported high echinoid densities, which can be prolific grazers of sessile recruits on hard surfaces (see Hutchings 1986 for sea urchin grazing pressure on reef invertebrates). Fish or echinoid exclusion devices were not considered in the current study, in part because the main focus was on the down-facing surface of the panels which only had a 2 cm gap to bedrock. No *M. niger* observed were small enough to access this and only very small echinoids could squeeze in. Observations made during the course of this study supported *M. niger* predation to be important, although crushing associated with boulder movement in wave action was also clearly common. One littoral boulder (~6 m³) observed in 2002 had either completely disintegrated or been moved in 2003. Such crushing of shore communities may have parallels to ice scour, which destroys communities (and settlement panels) in polar regions (Barnes, 1996; Bowden *et al.*, 2006). The taxa and patchiness

on the panels were similar to the established sessile taxa of the surrounding communities recorded by the surveys after 2 years but benthos density differences on panels (5400 ind m⁻²) vs the surrounding shore (82.6 ind m⁻²) suggests a severe (>99.8%) mortality level.

CONCLUSIONS

Ascension I. panels showing the highest levels of colonization showed seven times more space occupancy, double the recruit density and three times as many taxa than the panels showing the lowest recruitment success. Despite such a level of variability, which is not uncommon elsewhere, the overall level of colonization is clearly low. Even so the number of total recruits is low compared with elsewhere in the world, though coral recruitment was equivalent to the lower rates reported at other remote islands. Despite there being a substantial literature regarding the colonization of remote oceanic islands by terrestrial taxa and hermatypic corals, there is little information on other marine taxa. Even so it is clear that littoral/sub-littoral colonization of remote islands is impoverished and particularly so at young sites. As hypothesized colonization taxa with non-dispersive larvae were poorly represented at Ascension I. Adult community richness is essentially similar across the littoral zone on remote islands with the zone immediately above the shore being least colonized.

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