ORIGINAL ARTICLE

The first comprehensive description of the biodiversity and biogeography of Antarctic and Sub-Antarctic intertidal communities

Huw James Griffiths[1]* and Catherine Louise Waller[2]

[1]*British Antarctic Survey, Cambridge CB30ET, UK*, [2]*Centre for Environmental and Marine Sciences, University of Hull, Scarborough YO11 3AZ, UK*

ABSTRACT

Aim To describe the distribution of biodiversity and biogeographical patterns of intertidal organisms in southern temperate and polar waters. We hypothesized that there would be differences in community structure between the Antarctic, which is most affected by ice, and the Sub-Antarctic and other neighbouring regions. We also hypothesized that rafting and West Wind Drift will be the significant drivers of biogeographical patterns. Additionally, the size, age, isolation, volcanic or glacial history of a region and the presence of large, beach dwelling, mammals and birds would all play a role in determining the level of biodiversity observed.

Location South Atlantic, Indian and Pacific Oceans and the Southern Ocean.

Methods We examined all available intertidal records from the Antarctic and Sub-Antarctic with additional data from neighbouring regions for comparison and context. We compiled 3902 occurrences of 1416 species of high southern latitude intertidal organisms from 229 locations and used PRIMER 6 to perform multivariate statistical analyses.

Results The Antarctic and Sub-Antarctic are shown to be distinct biogeographical regions, with patterns driven by a small number of widely distributed species. These wide-ranging molluscs and macroalgae dominate the biogeographical structure of the Southern Ocean intertidal, most likely as a result of rafting in the Antarctic Circumpolar Current. East Antarctic intertidal habitats are potentially isolated by the Ross and Weddell Sea ice shelves but represent a great unknown in this biogeographical scheme.

Main Conclusions The view that the Antarctic intertidal is a lifeless desert does not hold true, with Antarctic Peninsula intertidal communities being richer and more diverse than those in southern South America and the Sub-Antarctic islands. Changing conditions in the Antarctic and Sub-Antarctic intertidal mean that a representative baseline is needed (acquired through standardized and quantitative sampling) to assess future changes and to detect any invasive species.

Keywords

climate change, island biogeography, macroalgae, mollusc, rafting, richness, Southern Ocean

*Correspondence: Huw James Griffiths, British Antarctic Survey, High Cross, Madingley Road, Cambridge CB30ET, UK.
E-mail: hjg@bas.ac.uk.

INTRODUCTION

With 87% of marine glacier fronts currently in retreat on the Antarctic Peninsula (Cook *et al.*, 2005; Scambos *et al.*, 2014; Wouters *et al.*, 2015) the Antarctic intertidal environment is undergoing dramatic changes. Glacial retreat has the potential to expose ever-increasing areas of rocky or sedimentary intertidal habitat (Clark *et al.*, 2015). In cool temperate regions the intertidal zone is often seen as the marine 'canary in the coal mine' with changes in

species ranges due to climate change (e.g. Helmuth *et al.*, 2006; Hawkins *et al.*, 2008) and establishment of invasive species being observed first (e.g. Griffiths *et al.*, 1992; Robinson *et al.*, 2005). So it comes as little surprise that one of the 80 key questions raised by the first Scientific Committee on Antarctic Research (SCAR) Antarctic and Southern Ocean Science Horizon Scan was: '*How will increases in the ice-free Antarctic intertidal zone impact biodiversity and the likelihood of biological invasions?*' (Kennicutt *et al.*, 2014).

The Antarctic intertidal environment is considerably less well sampled than either the surrounding deep sea (Brandt *et al.*, 2014) or adjacent terrestrial habitats (Chown *et al.*, 1998; Shaw *et al.*, 2010), the opposite situation of almost anywhere else in the world. From initial observations, the Antarctic littoral environment would appear to be virtually lifeless, with no visible zonation, one of the most obvious and defining features of rocky shores globally. It is characterized by intense seasonal scouring by ice, winter ice encasement, high UV radiation and seasonally large variations in temperature and salinity. However, despite the long-held view that the Antarctic intertidal conditions are too extreme to support obvious signs of macrofaunal life (Powell, 1965; Clark *et al.*, 2015), little known historic and recent studies show that intertidal communities can survive these extreme and harsh conditions.

The Sub-Antarctic intertidal environment is often characterized by highly exposed shores on extremely remote islands. The Sub-Antarctic Islands are situated in the path of the Antarctic Circumpolar Current and are subjected to the force of the southern Westerly winds (Nikula *et al.*, 2010). These habitats are often rocky or boulder beaches comprised of bedrock and ice-formed cobble pavements (Hansom, 1983b). Ice-free coastlines are often dominated by dense beds of the kelp *Durvillaea antarctica* (Frazer *et al.,* 2009; Nikula *et al.*, 2010) and other large macrophytes (Knox, 1960). Unlike shores further south, there is often a distinct pattern of zonation from extreme high water to low water spring tides (Simpson, 1976).

The earliest published record of Antarctic intertidal life dates back to the Belgian Antarctic Expedition of 1897-99 which collected two species of gastropod mollusc, *Nacella polaris* (formerly known as *N. concinna*) (Hombron & Jacquinot, 1841) and *Laevilitorina caliginosa* (Gould, 1849), and a single species of bivalve, *Mysella subquadrata* (Pelseneer, 1903) from the intertidal of Two Hummock Island off the West Antarctic Peninsula. During the Heroic Era of Antarctic Exploration, many national expeditions included biologists. None of these early expeditions concentrated explicitly on intertidal research; however, many opportunistically sampled the shores of Antarctica and the Sub-Antarctic. Later researchers and expeditions went on to undertake dedicated qualitative and quantitative research in the intertidal. The history of Southern Ocean intertidal research and references used to create the intertidal database are listed in Appendix S1.

Aims

The aims of this study are to draw together and synthesise all available data on the Antarctic and Sub-Antarctic intertidal biota and to determine if there are any commonalities between sites and regions.

We hypothesize that there will be differences in community structure between the high Antarctic, which is most affected by ice, and the Sub-Antarctic and other neighbouring regions. We also hypothesize that rafting and West Wind Drift will be significant drivers of biogeographical patterns. Additionally, the size, age, isolation, volcanic or glacial history of a region and the presence of large, beach dwelling, mammals and birds will all play a role in determining the level of biodiversity observed in the intertidal.

METHODS

In this study we examine all available whole community intertidal records from the Antarctic and Sub-Antarctic (following the geographical definitions used by the Scientific Committee on Antarctic Research Biogeographic Atlas). All islands south of the Polar Front are considered to be Antarctic (Bouvet Island, South Georgia, South Orkney Islands, South Sandwich Islands, South Shetland Islands) as described in Linse *et al.* (2006). All other islands within the influence of the Circumpolar Current are regarded as Sub-Antarctic (Fig. 1). The database was compiled from studies of the ecology or whole communities of localities and avoiding studies that only targeted single species or taxa. We compiled data for comparison from southern South America, the Falkland Islands, Tristan da Cunha, South Africa, Tasmania and southern New Zealand, although data from these comparison regions are not exhaustive.

The restriction of data to comparable community studies and avoiding data from single taxon studies inevitably means that some regions with existing published intertidal biodiversity knowledge, such as the New Zealand Sub-Antarctic Islands, are underrepresented in the database, results and conclusions. This is illustrated in Figs 2 and 3 where distributions for selected taxa are supplemented with additional data from sources not used in our analyses to illustrate that taxon-specific distributional data exist beyond the scope of our database.

We created a database of 3902 records of high southern latitude intertidal occurrences for 1416 species/taxa, verified using the World Register of Marine Species (WoRMS Editorial Board 2015), from 229 locations (Fig. 1). Records date back to 1897. The majority of data came from published manuscripts (see Appendix S1), with additional digital records from the Smithsonian Antarctic Invertebrates (http://invertebrates.si.edu/antiz/). For South Africa, we used the Natural Geography in Shore Areas (NaGISA) data set from the Global Biodiversity Information Facility (GBIF) (Rigby *et al.*, 2005). A record was considered to be intertidal if it
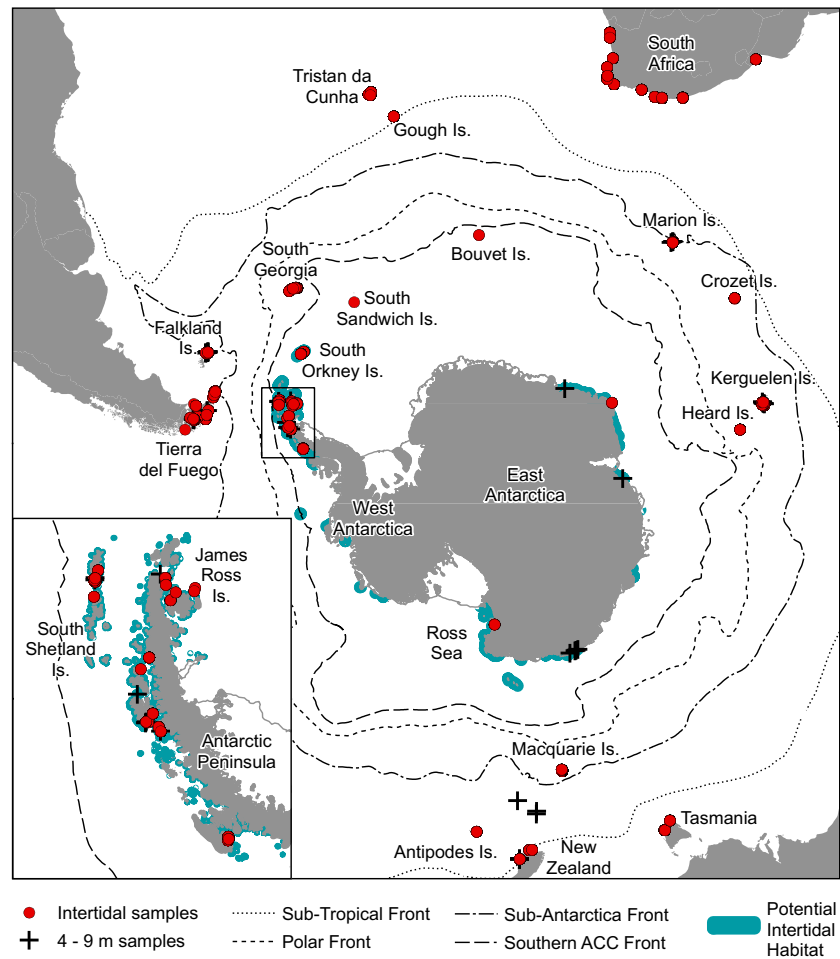
Figure 1 Intertidal records from the Southern Ocean and neighbouring regions. Projection: South Pole Stereographic.

was found between the high tide mark down to a maximum of 3 m depth (allowing for variable tidal range in Antarctica). All data used within this study are freely available through the open access www.biodiversity.aq website, the Antarctic regional node of the Ocean Biogeographic Information System (OBIS) and GBIF (http://www.gbif.org/data set/6bf0f3b3-053d-435d-ac96-1074625b937c).

The database was compiled using MS Access (2007) and data was mapped using ArcGIS 10 (Geographic Information System). PRIMER 6 software was used to analyse the biogeographical relationships between samples and to perform rarefaction analyses on species numbers for the best studied regions, using the most comparable records. Each locality within the primary area of interest was pre-assigned a set of hierarchical geographical groupings (Area – small geographical areas e.g. individual islands; Region – intermediate geographical areas e.g. island groups; Zones – large-scale geographical areas e.g. continental scale or oceanographic boundaries) to enable hypothesis testing using analysis of similarity (ANOSIM), multidimensional scaling (MDS) and similarity percentages (SIMPER). The faunal similarity between regions and between larger zones was quantitatively measured using Bray–Curtis similarities of presence/absence data and the significance of the geographical groupings was

assessed using the ANOSIM test (see Tables S2 & S3 in Appendix S3).

RESULTS

Biodiversity

Location/station data

The number of species per sampling location varied from a single species (from 16 locations across the study area) to over 100 species at each of the three islands of the Tristan da Cunha group (a single nominal location for each island for the records in the reports of the Norwegian Expedition in 1937–38). Just over half of all sampled locations (54%) had 10 or more species present. Molluscs were the most widespread phylum, recorded at 85% of locations, followed by arthropods (55%), chlorophytes and rhodophytes (green and red macroalgae) at 44% each and annelid worms present at 41% of locations. 727 (51%) of the 1416 species included in this study were only recorded at a single location and 95% of species were found at fewer than 10 locations. The most frequently reported species were the gastropod molluscs *Nacella polaris* (56 out of 98 Antarctic locations),
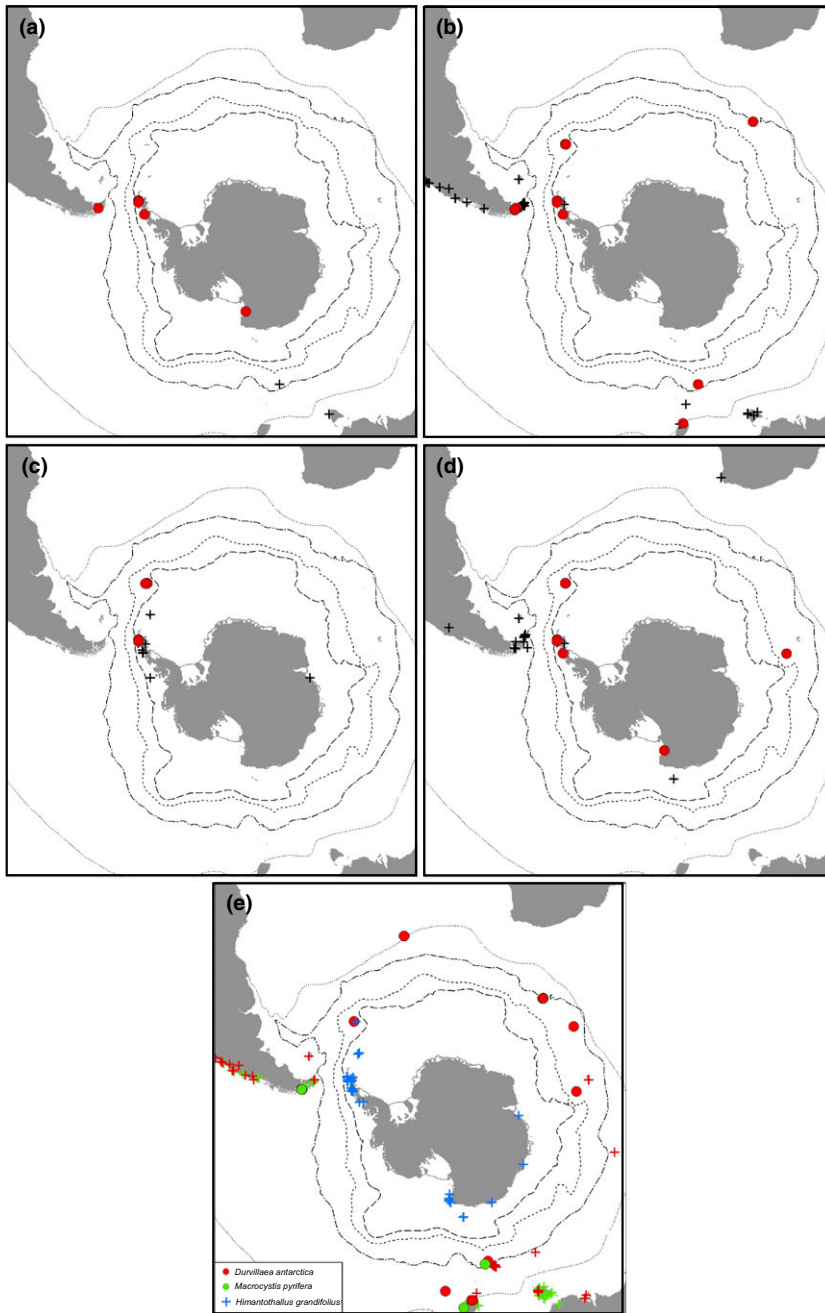
Figure 2 Distributions of commonly recorded macroalgal taxa: *Urospora penicilliformis* (a), *Adenocystis utricularis* (b), *Pyropia endiviifolia* (c), *Iridaea cordata* (d) and the large Southern Ocean kelp species; *Durvillaea antarctica*, *Macrocystis pyrifera* and *Himantothallus grandifolius* (e). Circles indicate intertidal records, crosses represent subtidal records and additional records from the Global Biodiversity Information Facility. Projection: South Pole Stereographic.

Laevilitorina caliginosa (45 locations) and the macroalga *Adenocystis utricularis* (34 locations) (Figs 2 & 3).

Regional data

Because sampling methods, protocols and reporting varied between studies comparisons of overall biodiversity between locations is difficult e.g. some reports focussed on animals only, some studies gave species lists for an entire survey while some gave detailed data by transect or quadrat. Numbers of animal species and sampled locations varied between regions, see Table 1. Pooling the species lists by geographical area allows for more meaningful comparisons between

regions. Comparisons of numbers of recorded intertidal animal phyla between geographical regions showed 13 phyla in Tierra del Fuego, 10 from the Antarctic Peninsula and Sub-Antarctic and 9 phyla from the South Orkney Islands, South Shetland Islands and New Zealand. East Antarctica had only 4 recorded animal phyla and single locations from the South Sandwich Islands and Bouvet Island recorded only gastropod molluscs (limpets of the genus *Nacella*) (Fig. 2). 81% of species were found intertidally only in a single geographical area. Only eight species spanned five or more geographical areas.

The relative diversity and dominance of animals at phylum level as a proportion of the total number of species per
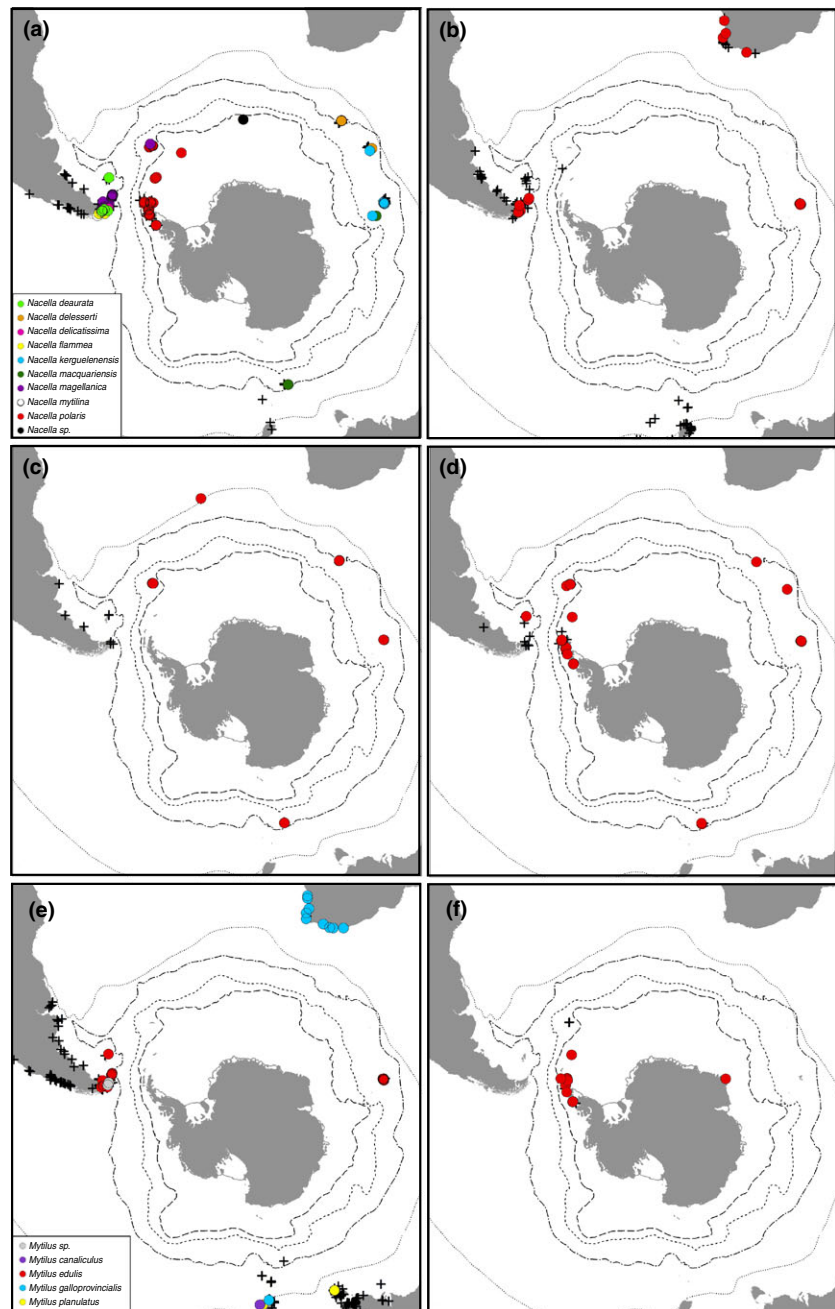
Figure 3 Distributions of commonly recorded animal taxa: the genus *Nacella* (a) *Aulacomya ater* (b) *Kerguelenella lateralis* (c) *Laevilitorina calignosa* (d) the genus *Mytilus* (e) and *Antarctonemertes valida* (f). Circles indicate intertidal records, crosses represent subtidal records and additional records from the Global Biodiversity Information Facility. Projection: South Pole Stereographic.

region (Fig. 4) shows no clear differences between the Antarctic and neighbouring regions. Poorly sampled areas with low numbers of recorded species show low levels of diversity and are dominated by few phyla (Bouvet Island, the South Sandwich Islands, East Antarctica and the New Zealand Sub-Antarctic Islands). Three phyla (molluscs, arthropods and annelid worms) are dominant in terms of numbers of species in most regions (Fig. 4). Total numbers of species per order in each geographical area are given in Table S1 in Appendix S2.

Species accumulation (rarefaction) curves for the better sampled geographical areas (Fig. 5) show no asymptote for any area. The islands of the Sub-Antarctic and King George Island show the lowest levels of biodiversity with the Macquarie Island and South Georgia curves being noticeably lower. The Sub-Antarctic Islands display between ~30 to ~70% lower biodiversity than the Antarctic Peninsula. The highest levels of biodiversity are seen in South Africa and New Zealand. The Antarctic Peninsula appears to have comparable or higher levels of biodiversity than the southern South American regions studied (Straits of Magellan, Tierra del Fuego and the Falkland Islands).

Biogeography

Regional patterns across the entire community (Fig. 6a) showed distinct groupings for South Africa, Tierra del Fuego and the majority of the Sub-Antarctic with the ANOSIM and

Table 1 A summary of the Antarctic and Sub-Antarctic intertidal biodiversity database records quantifying the data used for each of the major geographical regions included in the study.

Zone	Region	Total species	Studies	Sites
Antarctic	Antarctic Peninsula	185	13	30
	Bouvet Island	2	1	1
	East Antarctic	10	2	3
	South Georgia	78	7	27
	South Orkney Islands	56	3	4
	South Sandwich Islands	1	1	1
	South Shetland Islands	105	6	32
Antarctic Total		356	30	98
Falkland Islands Total		59	4	7
New Zealand Total		136	4	7
South Africa Total		282	1	16
Sub-Antarctic Total		329	12	58
Sub-Antarctic NZ Total		13	1	1
Tasmania Total		81	3	3
Tierra del Fuego Total		198	4	36
Tristan da Cunha Total		179	1	3

MDS showing some overlap between geographical regions and the Falkland Islands showing mixed affinities. The different Antarctic regions formed a single, well supported grouping on the larger zone level (Fig. 6b) but with a significant degree of overlap between regions. In particular, South Georgia seemed to display affinities for both the Sub-Antarctic and other Antarctic locations. The Antarctic Peninsula region formed a strong grouping but had significant overlap, as

might be expected, with the South Shetland and South Orkney Islands.

The results of the SIMPER analyses found that the most significant components driving the similarity by geographical area were the molluscs and macroalgae (see Table S4 in Appendix S3). The results showed that macroalgae dominated the patterns for Gough Island, the Straits of Magellan, King George Island and South Africa. Molluscs dominated the patterns of Tierra del Fuego, Signy Island, the Antarctic Peninsula, Kerguelen, Macquarie Island, Seymour Island and Adelaide Island. Both molluscs and algae determined the overall patterns of South Georgia and Anvers Island. The majority of these pattern-driving molluscs were gastropods from the genera *Nacella*, *Kerguelenella* and *Laevilitorina*; however, three species of bivalve; *Aulacomya ater* (Kerguelen), *Mysella subquadrata* (Anvers Island) and *Yoldia eightsii* (Seymour Island) formed significant components of different geographical areas.

Further analyses (Figs 6c & d and 6e & f) were conducted on the molluscs and macroalgae separately. Many of the overall patterns for the whole community held true for these selected taxa, including clear differentiation of South Africa and Tierra del Fuego. For both the molluscs and the algae the position of Tristan da Cunha and South Georgia seemed to be more distinct than for the whole community analyses. South Georgia seems to sit closer to the Sub-Antarctic in its algal community and closer to the Antarctic in its molluscan fauna. The depauperate Antarctic Peninsula algal community seems to show no clear grouping, unlike that of its near
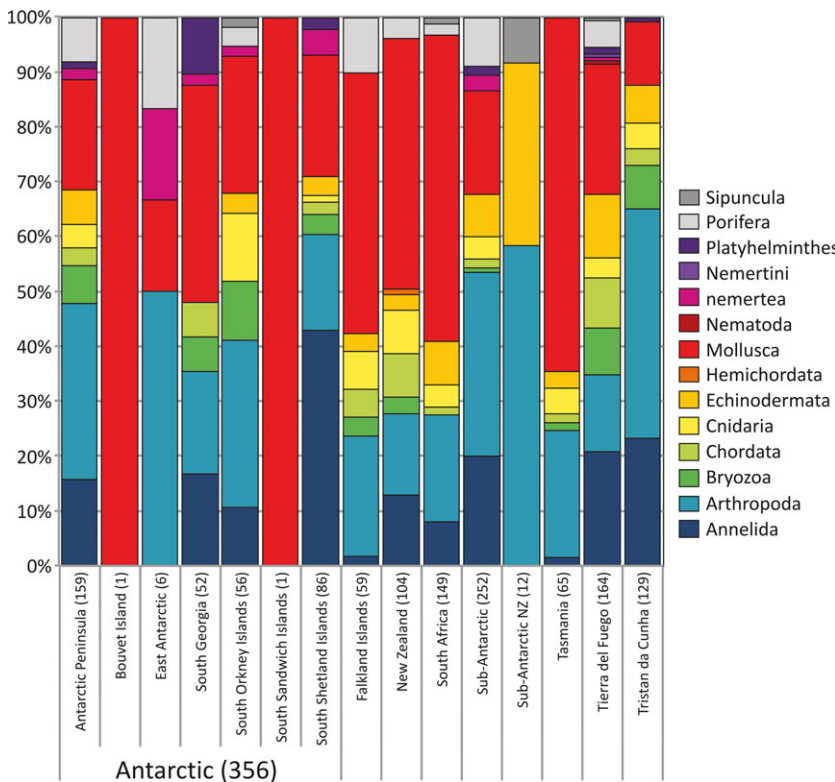
Figure 4 Relative richness (number of species) of animals at phylum level within the different regions. Total numbers of recorded intertidal animal species in brackets.
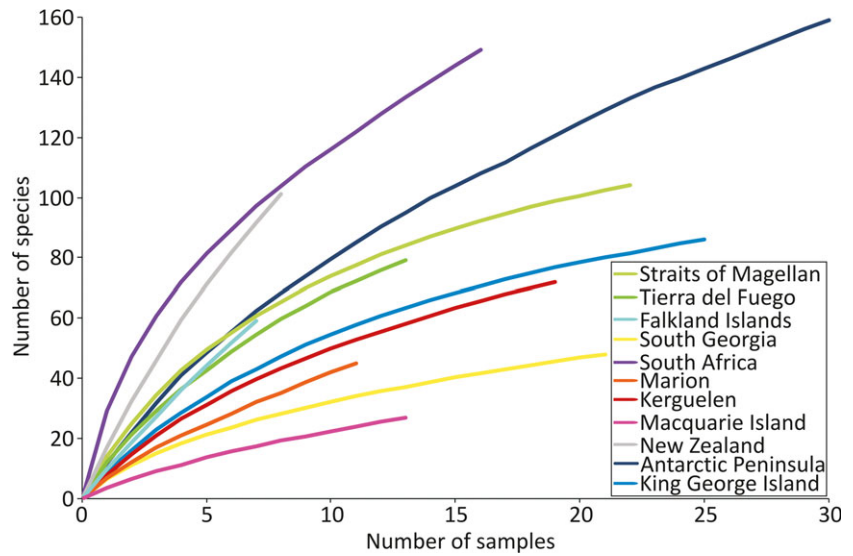
Figure 5 Species accumulation curves for the best sampled geographical areas of the study. Samples represent a single collection event. Studies that summarized multiple localities or sampling events as a single record were excluded from the analysis.
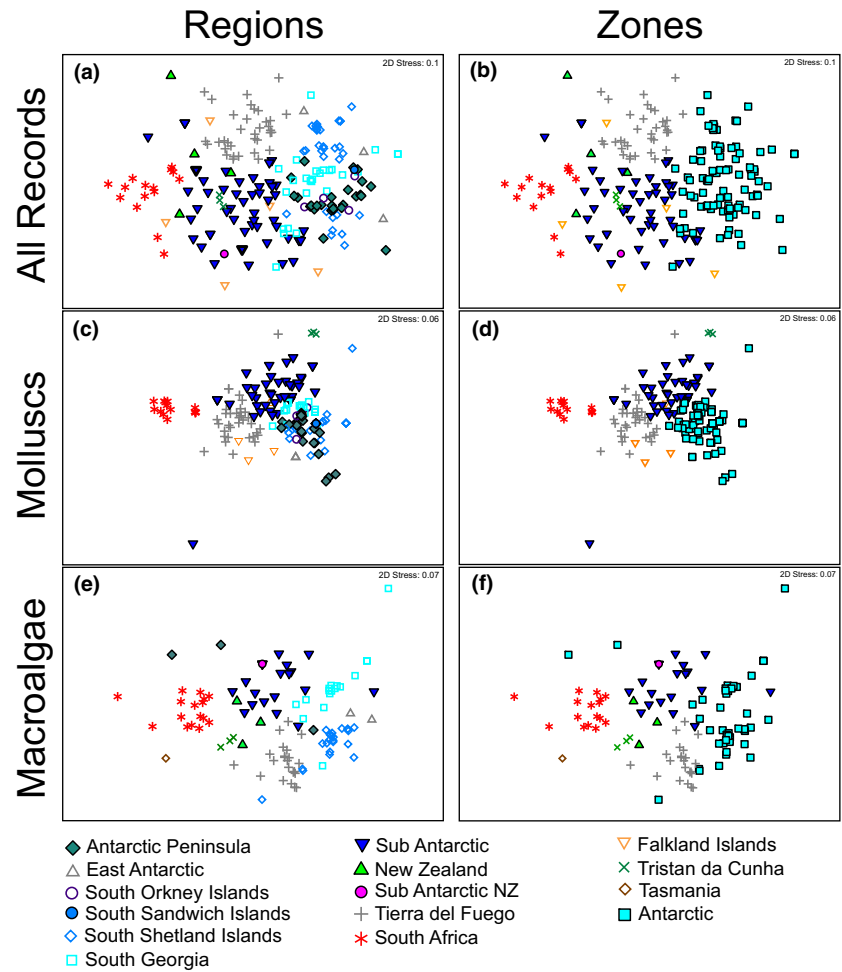
Figure 6 Similarity of all intertidal records (a & b), molluscs (c & d) and macroalgae (e & f) between locations using non-metric multidimensional scaling (NMDS) using Bray–Curtis similarities applied to species data.

neighbour the South Shetland Islands. No intertidal macroalgae were reported in the whole community studies from the Falkland Islands despite being known to exist from other algal focussed studies (Skottsberg, 1941) however the molluscan fauna is shown to group closely with that of Tierra del Fuego.

Some globally important intertidal groups, such as barnacles, are absent in this study and others, such as mytilid

mussels, are only found intertidally in the Sub-Antarctic from Kerguelen (Fig. 3e). Brachyuran crabs are famously absent from the Antarctic but are known from the intertidal of the Sub-Antarctic. The most widely distributed intertidal crab was *Halicarcinus planatus*, found from Tierra del Fuego to Kerguelen, although it has also been reported from the Falklands, Marion Island and Macquarie Island. A single intertidal example was reported by the Scottish National Expedition of 1903 from the South Orkney Islands (Griffiths *et al.*, 2013) and again recently in the shallow subtidal zone at Deception Island, South Shetland Islands (Aronson *et al.*, 2015). Intertidal kelp (*Macrocystis pyrifera* and *Durvillaea antarctica*) have not been found south of 55 degrees, the most common subtidal kelp found in the Antarctic is *Himantothallus grandifolius* (Fig. 2e).

DISCUSSION

Biodiversity

Many of the regional differences in recorded species numbers can be attributed to differing sampling effort and methodologies between studies. The relative inaccessibility and lack of national research bases means that locations such as the South Sandwich Islands, the New Zealand Sub-Antarctic, Bouvet and parts of East Antarctica are underrepresented in the database (Fig. 1). Other areas, such as Peter I Island, Elephant Island, Shag Rocks and many others, lack published intertidal community records.

The rarefaction analyses show that even when sampling is taken into account there are regional differences in species richness (Fig. 5). By far the most species-rich regions in this study were South Africa and southern New Zealand. This came as little surprise, given that their large geographical area, their known high marine species richness and high numbers of endemic species (Costello *et al.*, 2010). The lower diversity observed from the Patagonian intertidal also reflects its comparatively low recorded overall marine species richness (Costello *et al.*, 2010; Linse *et al.*, 2006; Barnes & Griffiths, 2008). The little-studied intertidal fauna of the Falkland Islands showed similar diversity levels to that of Tierra del Fuego, which would be expected given its geographical location.

Sub-Antarctic Biodiversity

The islands of the Sub-Antarctic with sufficient sampling effort for rarefaction analysis were Marion, Kerguelen and Macquarie. These islands represented three out of the four lowest species richnesses observed in this study. The island biogeography rule (MacArthur & Wilson, 1967) states that species richness typically increases with geographical area and decreases with isolation. This would go some way to explaining the pattern observed for these Sub-Antarctic islands with the largest island, Kerguelen, being the richest and the smallest, Macquarie Island, being the least diverse (Fig. 5, Table 2). The geological ages of these islands vary between 0.45 and 30 million years; however, González-Wevar *et al.* (2014) showed that the youngest island, Marion, was colonized very shortly after its emergence. The islands also have similar glacial histories, with Kerguelen likely to have been most heavily glaciated and the last to begin deglaciation (Fraser *et al.*, 2009). Given that Kerguelen has the highest species richness it appears that its glacial history has not significantly impacted its biodiversity compared to other Sub-Antarctic islands. Extreme geographical isolation and a common glacial history appear to be the major factors determining the low intertidal biodiversity of these Sub-Antarctic Islands.

Table 2 Geographical position, age, isolation, temperature and glacial context of the main study areas for Antarctic and Sub-Antarctic intertidal communities (adapted from Chown *et al.*, 1998; Ó Cofaigh *et al.*, 2014; Hodgson *et al.*, 2014 and Mackintosh *et al.*, 2014). For glaciation rank: 1 = no glaciation, 11 = completely ice covered, and indicates extent of past glaciations of the southern ocean islands.

Region	Position		Area (km²)	Age (myr)	Distance from continent (km)	Distance from Antarctica (km)	SST (°C)	Glaciation (rank)	Deglaciation age (years)
Tristan da Cunha	37.1 °S	12.25 °W	102	18	2820	4000	15.3	1	N/A
Gough	40.33 °S	9.54 °W	57	6	2670	3550	12.4	1	N/A
Antipodes	49.68 °S	178.77 °E	21	0.5	872	2580	7.9	1	N/A
Marion	46.9 °S	36.75 °E	290	0.45	1900	2500	5.5	6	17–2.3k
Crozet	46.42 °S	51.63 °E	280	8.1	2740	2350	4.8	2	11k
Kerguelen	49.37 °S	69.5 °E	7200	30	4110	2100	3.5	9	15k–present
Bouvet	54.43 °S	51.85 °W	49	1.39	2900	1700	−0.3	11	?
Macquarie	54.62 °S	158.9 °E	128	11.5	990	1600	5.1	2	17–8k
South Sandwich Is.	59.03 °S	26.52 °W	337	4	2600	1600	0.5	10	?
South Georgia	54.25 °S	37.0 °W	3755	120	2210	1500	1.5	11	19k–present
Heard	53.1 °S	73.5 °E	368	20	4570	1500	1.7	11	?–present
West Falkland	51.5 °S	60.5 °W	3500	3000	530	1250	7.7	2	N/A
South Orkney Is.	60.58 °S	45.5 °W	620	185	1400	600	−1.0	11	11.5k–present
King George Island	62.03 °S	58.35 °W	1150	106	900	120	0.5	11	15k–present
Antarctic Peninsula	–	–	–	300	1000	–	−0.5	11	10k–present
East Antarctica	–	–	–	2500	2800	–	−1.8	11	14k–present

Antarctic Biodiversity

The Antarctic Peninsula is one of the better studied regions with 185 species recorded from 30 localities and a species richness higher than that of the Patagonian regions and the Sub-Antarctic. This is despite having some of the youngest deglaciation ages (Table 2) and high levels of winter and some summer sea ice. The sites furthest south (and therefore experiencing the highest disturbance due to ice encasement in winter and scour in summer) have a surprisingly high diversity, despite superficially appearing to be sparsely populated. Most species survive below the upper scoured surface of the cobble boulder matrix (Waller et al., 2006; Waller, 2013). It is likely that these cobble pavements are a relatively common feature where ice encasement occurs. Hansom (1983a,b) reported the presence of these structures at both the South Shetland Islands and various sites on the northwest coast of South Georgia. He estimated that they may have been present for at least 9000 years, providing a stable and protected environment for cryptic communities to become established.

King George Island shares 27% of its species with the Antarctic Peninsula and has higher biodiversity than Kerguelen, which is over six times larger. The intertidal species richness of King George Island is higher than that of any other Antarctic or Sub-Antarctic island in this study. This could be attributed to its geographical closeness to the Antarctic Peninsula. Although it does not have as high overall biodiversity as the neighbouring Peninsula, it has 19 species of macroalgae compared with the 12 found around the Peninsula.

The intertidal biodiversity of the Antarctic island of South Georgia is lower than expected if the theory of island biogeography is applied. Given its geographical locality (relatively near to both South America and Antarctica), its large geographical size, significant age and relatively early deglaciation, it would be reasonable to expect South Georgia to be among the most diverse islands in the study. It is, in fact, the second least diverse area analysed, after Macquarie Island. Marion Island, for example, is 13 times smaller than South Georgia and 400 km further from any continent yet the intertidal biodiversity is ~20% higher. South Georgia's intertidal biodiversity is also far lower than that of the other well studied Antarctic regions. It has 37% of the richness of the Antarctic Peninsula for a given number of samples and 60% of that of the far smaller King George Island. Assuming that intertidal species richness is relative to overall marine species richness for an area, then South Georgia would be expected to have higher biodiversity than any of the other Antarctic or Sub-Antarctic areas in this study (Linse et al., 2006).

The intertidal organisms of South Georgia may be suppressed by physical disturbance and nutrient input from some of the island's other inhabitants. Bonner (1985) attributed damage to vegetation on land and high levels of 'manuring' to fur seals. The current South Georgia population is estimated to be over 3 million breeding individuals. Along with the intense physical damage, this large seal population results in raised levels of nutrients from waste products. Increased nutrient levels from large colonies of animals have been shown to have a negative effect on intertidal biodiversity elsewhere (Wootton, 1991). Barnes et al. (2006) and Waller (2008) observed seals at every locality of their South Georgia studies and remarked upon the sparsity of intertidal life at Bird Island, which they attributed to trampling by fur seals. However, they also commented on the diversity of life on a boulder area of the same beach that was populated by 14 species representing nine classes, including gastropods present in their hundreds per metre square (Barnes et al., 2006). Given that the areas of South Georgia studied for intertidal organisms are in the north and west of the island, coincident with the main fur seal population (Boyd, 1993), then our levels of intertidal biodiversity for the island may be an underestimate. Another contributing factor to the low biodiversity may be that South Georgia has glaciers that calve into some bays leading to potential localized ice scour (Pugh & Davenport, 1997).

East Antarctica is probably the least studied intertidal area of any continent on Earth. With only three sampled intertidal locations with records of just six species of animal and four species of seaweed, it is difficult to judge whether the East Antarctic intertidal is virtually devoid of life as previous authors have stated (e.g. Knox, 1960) or if it is merely largely unsampled. Figure 1 shows that there are numerous localities in East Antarctica that have potential intertidal habitats, and shallow subtidal records from these regions confirm diverse life as shallow as 2 metres (Australasian Antarctic Expedition 1911-14, BANZARE Expedition 1931, Gruzov et al., 1967; Kirkwood & Burton, 1988). If there is an extensive intertidal fauna in East Antarctica it is likely to be isolated from that of West Antarctica by the extensive areas of rock free coast, deep shelf waters and floating ice shelves of the Ross and Weddell Sea regions and from the Sub-Antarctic by large expanses of deep water and fast moving currents (Fig. 1).

Biogeography

The overall pattern of distinct Antarctic and Sub-Antarctic intertidal biogeographical regions, both having a degree of species overlap with southern South America and each other, is similar to that found in the subtidal communities (Griffiths et al., 2009; Koubbi et al., 2014). The low subtidal connectivity observed between these regions and South Africa, Tasmania and New Zealand is also reflected in the intertidal records (Fig. 6). These patterns, given the glacial history of many of the geographical areas (Table 2), are more likely to reflect relatively recent oceanographic connections (González-Wevar et al., 2014) rather than the ancient Gondwanan break up signatures of deeper waters (Griffiths et al., 2009).

Given that the majority of species (51%) were only recorded intertidally at a single location and only 5% of species were recorded at ten or more locations, it is no surprise that a small number of well distributed species are driving

the regional and larger scale biogeographical patterns. Although none of these species are obligate intertidal organisms, all have known distributions from coastal regions with none previously being reported from the deep sea (Figs 2 & 3). Therefore, their distributions must be driven by shallow or surface currents either through larval transport, rafting or by swimming/walking shorter distances between suitable habitats.

Compared with the Sub-Antarctic subtidal, intertidal areas shared a lower percentage of species. Griffiths et al. (2009) found up to 50% of sublittoral species were shared between Sub-Antarctic islands but we found intertidal locations had a maximum of around 31%. Higher percentages of shared species were found between Antarctic intertidal regions but not as high as observed for the subtidal (Griffiths et al., 2009). The high number of species recorded only once implies that a wide range of species appear to be opportunistically exploiting the intertidal (potentially as nursery grounds, feeding grounds or to avoid predation) and is also probably a reflection of the generally low numbers of samples. Juvenile Pagothemia borchgevinki (Antarctic icefish) have been observed in shallow pools in the intertidal around Rothera Research Station (Adelaide Island) (pers ob.).

Nacella polaris is the most frequently reported species in this study and is the most significant species driving the Antarctic intertidal grouping, accounting for 38% of the observed similarity between locations. It has a wide distribution within the West Antarctic and Scotia Sea region. Other species of the genus Nacella have South American and Sub-Antarctic distributions (González-Wevar et al., 2014) (Fig. 3a). The known distribution of N. polaris is restricted by availability of shallow/intertidal rocky substrata. The lack of records from the East Antarctic can be attributed to the distances between existing populations in West Antarctica and any suitable habitat in the East (Fig. 1). Although the distances to the islands of the Scotia Sea seem equally great, near-surface ocean drifters only take 4-8 months to cross Scotia Sea from Antarctic Peninsula to South Georgia (Thorpe et al., 2004). Although N. polaris has a long lived, ~2 month, planktonic larval phase (Bowden et al., 2006) this is not long enough to explain its current distributional pattern. For the species to have populations throughout the Scotia Sea would require a longer term transport mechanism such as rafting. The geological age of Marion Island (~0.45 Ma) was found by González-Wevar et al. (2014) to be consistent with that of the resident limpet species, Nacella delesserti. Nacella delesserti separated from its sister species, N. polaris, when it colonized Marion Island. Given the life history of N. polaris it is impossible for larval transport alone to explain this colonisation.

The most likely natural conduit for rafting organisms in the region is macroalgae. Smith (2002) estimated that over 70 million kelp rafts are afloat between 46 and 53 degrees south at any one time. All of the significant pattern-driving species of the Antarctic and Sub-Antarctic were molluscs or macroalgae. Several of the key animal species distributions (Laevilitorina calignosa, Kerguelenella lateralis and the genera Nacella and Mytilus) reflect the distribution of kelp (Durvillaea antarctica and Macrocystis pyrifera). Although these two large kelp species are absent from the Antarctic, another species, Himantothallus grandifolius, is circumpolar and may play a role in transporting shallow water species around the continent.

Fraser et al.'s (2009) circum-Sub-Antarctic analyses of DNA variation in Durvillaea antarctica support the hypothesis that this species only recently recolonized the Sub-Antarctic. The species exhibits a striking degree of genetic homogeneity in this region compared with lower latitudes. Recolonization is likely to have involved a series of long-distance rafting events of the buoyant kelp from remote source populations. They also suggest that Sub-Antarctic kelp was eliminated during the LGM. Similarly, the molecular results for Macrocystis pyrifera showed shared haplotypes among some of the Sub-Antarctic islands and southern-central Chile, suggesting a recent colonization of the Sub-Antarctic region (Macaya & Zuccarello, 2010).

Nikula et al. (2010) suggest that macroalgal rafting may explain similarities in the species composition of intertidal marine communities across the Sub-Antarctic. They attributed the low genetic differentiation of kelp-dwelling crustaceans in the Sub-Antarctic to rafting. Leese et al. (2010) examined gene flow in an isopod found around South Georgia, Bouvet, and Marion Islands. They concluded that rare long-distance dispersal via rafting, rather than vicariance or human-mediated transport, must be responsible for the observed molecular patterns. There is a distinct lack of knowledge as to how long species can survive while rafting in the open ocean but Fraser et al. (2011) documented 10 species of invertebrates rafting for several weeks between New Zealand and the neighbouring Sub-Antarctic islands, covering a distance of at least 400 km. Helmuth et al. (1994) found large numbers of kelp rafts in the Scotia Sea and believed that rafting was responsible for the distribution of the bivalve Gaimardia trapesina. They estimated that kelp from South America would reach South Georgia by passive rafting after 100 days afloat travelling over 3700 km.

These proposed natural pathways both into and out of Antarctica and around the Sub-Antarctic are dependent on the Antarctic Circumpolar Current and dispersal through West Wind Drift (Waters, 2008). There is a low probability that an individual raft will ever make landfall at localities with suitable conditions, given the vastness of the Southern Ocean and small size of the islands. However, once established, early colonizers face little competition for space and resources and may thrive (Waters et al., 2013). For example, the low species diversity of the Sub-Antarctic intertidal and the low numbers of pattern-driving species also suggests that not all species are capable of rafting such great distances. Species which live on or in large kelp would be advantaged by this process.

The anthropogenic equivalent of kelp rafting is litter, particularly plastics. Fishing operations in the Southern Ocean have been identified as the major source of marine debris found on the coasts of Antarctica, but plastics from lower

latitudes may also cross the Polar Front (do Sul *et al.*, 2011). These plastics have been demonstrated to support a variety of marine life for extended periods of time, even in Antarctic waters (Barnes & Fraser, 2003). Rafting on litter is, like kelp rafting, a passive process controlled by ocean currents and is unlikely to enable a wider range of species to colonize the Antarctic and Sub-Antarctic.

Journeys by ship can take less than 4% of the time it would take to reach the same destination by rafting. Assuming that an organism is capable of surviving the conditions at its destination, transport on the hulls or in the ballast water of ships removes the need to survive long, slow journeys across the open ocean (Lewis *et al.*, 2003). Indeed Lee & Chown (2007) found mytilid gastropods on a research ship's hull that may have survived several trips to the Antarctic. This method of transport could open up the Antarctic and Sub-Antarctic intertidal to a completely new range of colonizers that would not survive rafting. Clayton *et al.* (1997) reported five cosmopolitan algal species and two North Atlantic species (*Porphyra linearis* and *Enteromorpha intestinalis*) from sites on Deception Island and Half Moon Island (South Shetland Islands). *Enteromorpha* spp. are common fouling organisms and it is possible that they were transported on ships hulls and found the volcanically heated waters of Deception Island a suitable environment to survive in. It may be that over time and with changing environmental conditions on the Peninsula they will adapt and spread. Because of this these species may act as useful indicators of climate change in Antarctic intertidal habitats.

With currently warming conditions along the Antarctic Peninsula it is likely that there will be a phase shift from the existing microalgal biofilm (phytoplankton) (e.g. Pugh & Davenport, 1997) to macroalgal dominated shores (Skottsberg, 1941). There are locations in the South Shetland Islands (e.g. Byers Peninsula, Livingston Island) that already exhibit complex macroalgal communities with evidence of zonation (Waller, unpublished data). This potential change in habitat complexity and reduced impact from sea ice has consequences for the establishment of a rich and diverse ecosystem which would be much more hospitable to any non-native species that are transported into Antarctic waters. The presence of juvenile Antarctic icefish, which were thought to be highly stenothermal, in the intertidal at Adelaide Island (where temperatures have been recorded as high as 7 °C in pools) suggests that these species have the physiological capacity to exploit these previously unconsidered habitats.

It is impossible to track and measure any future changes in diversity and species distribution without an adequate baseline. The changing environment and increasing habitat availability make this an issue that requires urgent study.

CONCLUSIONS

The major issue faced when studying the biogeography and biodiversity of the Antarctic and Sub-Antarctic intertidal is the lack of standardized and comparable quantitative data.

The view that the Antarctic intertidal is virtually devoid of macrofaunal life does not hold true with Antarctic Peninsula intertidal communities being richer and more diverse than those in southern South America and Sub-Antarctic islands. This relatively rich community includes 159 recorded species from 13 different phyla.

The Antarctic and Sub-Antarctic are distinct biogeographical regions, with patterns driven by a small number of widely distributed species. These wide-ranging molluscs and macroalgae dominate the biogeographical structure of the Southern Ocean intertidal, most likely as a result of long-distance rafting in the Antarctic Circumpolar Current. Changing conditions in the Antarctic and Sub-Antarctic intertidal mean that a representative baseline is required, acquired through standardized and quantitative sampling, to assess future changes and to detect any invasive species.

REFERENCES

Aronson, R.B., Frederich, M., Price, R. & Thatje, S. (2015) Prospects for the return of shell-crushing crabs to Antarctica. *Journal of Biogeography*, **42**, 1–7. doi:10.1111/jbi.12414.

Barnes, D.K. & Fraser, K.P. (2003) Rafting by five phyla on man-made flotsam in the Southern Ocean. *Marine Ecology Progress Series*, **262**, 289–291.

Barnes, D.K. & Griffiths, H.J. (2008) Biodiversity and biogeography of southern temperate and polar bryozoans. *Global Ecology and Biogeography*, **17**, 84–99.

Barnes, D.K., Linse, K., Waller, C., Morely, S., Enderlein, P., Fraser, K.P. & Brown, M. (2006) Shallow benthic fauna communities of South Georgia Island. *Polar Biology*, **29**, 223–228.

Bonner, W.N. (1985) Impact of fur seals on the terrestrial environment at South Georgia. *Antarctic nutrient cycles and food webs* (ed. by W.R. Siegfried, P.R. Condy and R.M. Laws), pp. 641–646. Springer Science & Business Media, Berlin Heidelberg.

Bowden, D.A., Clarke, A., Peck, L.S. & Barnes, D.K.A. (2006) Antarctic sessile marine benthos: colonization and growth on artificial substrata over 3 years. *Marine Ecology Progress Series*, **316**, 1–16.

Boyd, I.L. (1993) Pup production and distribution of breeding Antarctic fur seals (*Arctocephalus gazella*) at South Georgia. *Antarctic Science*, **5**, 17–24.

Brandt, A., deVan Putte, A. & Griffiths, H. (2014) Southern Ocean benthic deep-sea biodiversity and biogeography. In: *Biogeographic Atlas of the Southern Ocean* (eds C. De Broyer, P. Koubbi, H.J. Griffiths, B. Raymond, C. D'Udekem D'Acoz, deVan Putte A., B. Danis, B. David, S. Grant, J. Gutt, C. Held, G. Hosie, F. Heuttmann, A. Post and Y. Ropert-Coudert). pp. 233–239. Scientific Committee on Antarctic Research, Cambridge.

Chown, S., Gremmen, N. & Gaston, K. (1998) Ecological biogeography of Southern Ocean islands: species-area relationships, human impacts, and conservation. *The American Naturalist*, **152**, 562–575.

Clark, G.F., Raymond, B., Riddle, M.J., Stark, J.S. & Johnston, E.L. (2015) Vulnerability of Antarctic shallow invertebrate-dominated ecosystems. *Austral Ecology*, **40**, 482–491.

Clayton, M.N., Wiencke, C. & Klöser, H. (1997) New records of temperate and sub-Antarctic marine benthic macroalgae from Antarctica. *Polar Biology*, **17**, 141–149.

Cofaigh, C.Ó., Davies, B.J., Livingstone, S.J., Smith, J.A., Johnson, J.S., Hocking, E.P., Hodgson, D.A., Anderson, J.B., Bentley, M.J., Canals, M., Domack, E., Dowdeswell, J.A., Evans, J., Glasser, N.F., Hillenbrand, C.D., Larter, R.D., Roberts, S.J. & Simms, A.R. (2014) Reconstruction of ice-sheet changes in the Antarctic Peninsula since the Last Glacial Maximum. *Quaternary Science Reviews*, **100**, 87–110.

Cook, A.J., Fox, A.J., Vaughan, D.G. & Ferrigno, J.G. (2005) Retreating glacier fronts on the Antarctic Peninsula over the past half-century. *Science*, **308**, 541–544.

Costello, M.J., Coll, M., Danovaro, R., Halpin, P., Ojaveer, H. & Miloslavich, P. (2010) A census of marine biodiversity knowledge, resources, and future challenges. *PLoS ONE*, **5**, e12110.

Fraser, C.I., Nikula, R., Spencer, H.G. & Waters, J.M. (2009) Kelp genes reveal effects of subantarctic sea ice during the Last Glacial Maximum. *Proceedings of the National Academy of Sciences USA*, **106**, 3249–3253.

Fraser, C.I., Nikula, R. & Waters, J.M. (2011) Oceanic rafting by a coastal community. *Proceedings of the Royal Society B: Biological Sciences*, **278**, 649–655.

González-Wevar, C.A., Chown, S.L., Morley, S., Coria, N., Saucéde, T. & Poulin, E. (2014) Out of Antarctica: quaternary colonization of sub-Antarctic Marion Island by the limpet genus *Nacella* (Patellogastropoda: Nacellidae). *Polar Biology*, **39**, 1–13.

Griffiths, C.L., Hockey, P.A.R., Van Erkom Schurink, C. & Le Roux, P.J. (1992) Marine invasive aliens on South African shores: implications for community structure and trophic functioning. *South African Journal of Marine Science*, **IB**, 713–722.

Griffiths, H.J., Barnes, D.K. & Linse, K. (2009) Towards a generalized biogeography of the Southern Ocean benthos. *Journal of Biogeography*, **36**, 162–177.

Griffiths, H.J., Whittle, R.J., Roberts, S.J., Belchier, M. & Linse, K. (2013) Antarctic Crabs: Invasion or Endurance? *PLoS ONE*, **8**, e66981. doi:10.1371/journal.pone.0066981.

Gruzov, Y.N., Propp, M.V. & Pushkin, A.F. (1967) Biological associations of coastal areas of the Davis Sea (based on the observations of divers). *Soviet Antarctic Expedition Info Bulletin*, **6**, 523–533.

Hansom, J.D. (1983a) Shore-platform development in the South Shetland Islands, Antarctica. *Marine Geology*, **53**, 211–229.

Hansom, J.D. (1983b) Ice-formed intertidal boulder pavements in the sub-Antarctic. *Journal of Sedimentary Research*, **53**, 135–145.

Hawkins, S.J., Moore, P.J., Burrows, M.T., Poloczanska, E., Mieszkowska, N., Herbert, R.J.H., Jenkins, S.R., Thompson, R.C., Genner, M.J. & Southward, A.J. (2008) Complex interactions in a rapidly changing world: responses of rocky shore communities to recent climate change. *Climate Research*, **37**, 123–133.

Helmuth, B., Veit, R.R. & Holberton, R. (1994) Long-distance dispersal of a subantarctic brooding bivalve (Gaimardia trapesina) by kelp-rafting. *Marine Biology*, **120**, 421–426.

Helmuth, B., Mieszkowska, N., Moore, P. & Hawkins, S.J. (2006) Living on the edge of two changing worlds: forecasting the responses of rocky intertidal ecosystems to climate change. *Annual Review of Ecology, Evolution, and Systematics*, **37**, 373–404.

Hodgson, D.A., Graham, A.G., Roberts, S.J., *et al.* (2014) Terrestrial and submarine evidence for the extent and timing of the Last Glacial Maximum and the onset of deglaciation on the maritime-Antarctic and sub-Antarctic islands. *Quaternary Science Reviews*, **100**, 137–158.

Kennicutt, M.C., Chown, Steven L., Cassano, J.J., Liggett, D., Massom, R., Lloyd, S. & Peck, L.S. (2014) Six priorities for Antarctic science. *Nature*, **512**, 23–25.

Kirkwood, J.M. & Burton, H.R. (1988) Macrobenthic species assemblages in Ellis Fjord, Vestfold Hills, Antarctica. *Marine Biology*, **97**, 445–457.

Knox, G.A. (1960) Littoral ecology and biogeography of the southern oceans. *Proceedings of the Royal Society of London Series B, Biological Sciences*, **152**, 577–624.

Koubbi, P., De Broyer, C., Griffiths, H.J., Raymond, B., D'Udekem D'Acoz, C., deVan Putte, A., Danis, B., David, B., Grant, S., Gutt, J., Held, C., Hosie, G., Heuttmann, F., Post, A., Ropert-Coudert, Y., Stoddart, M., Swadling, K.M. & Wadley, V. (2014) Conclusions: Present and Future of Southern Ocean Biogeography. In: *Biogeographic Atlas of the Southern Ocean* (eds C. De Broyer, P. Koubbi, H.J. Griffiths, B. Raymond, C. D'Udekem D'Acoz, A. Van de Putte, B. Danis, B. David, S. Grant, J. Gutt, C. Held, G. Hosie, F. Heuttmann, A. Post and Y. Ropert-Coudert). pp. 470–475, Scientific Committee on Antarctic Research, Cambridge.

Lee, J.E. & Chown, S.L. (2007) *Mytilus* on the move: transport of an invasive bivalve to the Antarctic. *Marine Ecology, Progress Series*, **339**, 307–310.

Leese, F., Agrawal, S. & Held, C. (2010) Long-distance island hopping without dispersal stages: transportation across major zoogeographic barriers in a Southern Ocean isopod. *Naturwissenschaften*, **97**, 583–594.

Lewis, P.N., Hewitt, C.L., Riddle, M. & McMinn, A. (2003) Marine introductions in the Southern Ocean: an unrecognised hazard to biodiversity. *Marine Pollution Bulletin*, **46**, 213–223.

Linse, K., Griffiths, H.J., Barnes, D.K. & Clarke, A. (2006) Biodiversity and biogeography of Antarctic and sub-Antarctic mollusca. *Deep Sea Research Part II: Topical Studies in Oceanography*, **53**, 985–1008.

MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton University Press, Princeton.

Macaya, E.C. & Zuccarello, G.C. (2010) Genetic structure of the giant kelp *Macrocystis pyrifera* along the southeastern Pacific. *Marine Ecology Progress Series*, **420**, 103–112.

Mackintosh, A.N., Verleyen, E., O'Brien, P.E., *et al.* (2014) Retreat history of the East Antarctic Ice Sheet since the last glacial maximum. *Quaternary Science Reviews*, **100**, 10–30.

Nikula, R., Fraser, C.I., Spencer, H.G. & Waters, J.M. (2010) Circumpolar dispersal by rafting in two subantarctic kelp-dwelling crustaceans. *Marine Ecology Progress Series*, **405**, 221–230.

Powell, A.W.B. (1965) Mollusca of Antarctic and Subantarctic seas. *Biogeography and ecology in Antarctica* (ed. by J. van Mieghem and P. van Oye), pp. 333–380. Springer, Netherlands.

Pugh, P.J.A. & Davenport, J. (1997) Colonization vs. disturbance: the effects of sustained ice-scouring on intertidal communities. *Journal of Experimental Marine Biology and Ecology*, **210**, 1–21.

Rigby, P.R., Konar, B., Kato, T., Iken, K., Chenelot, H. & Shirayama, Y. (2005) NaGISA OBIS Dataset ver.1

Robinson, T.B., Griffiths, C.L., McQuaid, C.D. & Rius, M. (2005) Marine alien species of South Africa—status and impacts. *African Journal of Marine Science*, **27**, 297–306.

Scambos, T.A., Berthier, E., Haran, T., Shuman, C.A., Cook, A.J., Ligtenberg, S. & Bohlander, J. (2014) Detailed ice loss pattern in the northern Antarctic Peninsula: widespread decline driven by ice front retreats. *The Cryosphere*, **8**, 2135–2145.

Shaw JD, Spear D, Greve M, Chown SL. (2010) Taxonomic homogenization and differentiation across Southern Ocean Islands differ among insects and vascular plants. *Journal of Biogeography*, **37**, 217–228.

Simpson, R.D. (1976) Physical and biotic factors limiting the distribution and abundance of littoral molluscs on Macquarie Island (sub-Antarctic). *Journal of Experimental Marine Biology and Ecology*, **21**, 11–49.

Skottsberg C. (1941) Communities of marine algae in sub-antarctic and Antarctic waters. *Kungliga Svenska Vetenskapsakademien Handlingar*, **91**, 1–95.

Smith, S.D. (2002) Kelp rafts in the Southern Ocean. *Global Ecology and Biogeography*, **11**, 67–69.

do Sul, J.A.I., Barnes, D.K., Costa, M.F., Convey, P., Costa, E.S. & Campos, L. (2011) Plastics in the Antarctic environment: Are we looking only at the tip of the iceberg? *Oecologica Australis*, **15**, 150–170.

Thorpe, S.E., Heywood, K.J., Stevens, D.P. & Brandon, M.A. (2004) Tracking passive drifters in a high resolution ocean model: implications for interannual variability of larval krill transport to South Georgia. *Deep Sea Research Part I: Oceanographic Research Papers*, **51**, 909–920.

Waller CL. (2008) Variability in intertidal communities along a latitudinal gradient in the Southern Ocean. *Polar Biology*, **31**: 809–816.

Waller, C.L. (2013) Zonation in a cryptic Antarctic intertidal macrofaunal community. *Antarctic Science*, **25**, 62–68.

Waller, C.L. (2008) Variability in intertidal communities along a latitudinal gradient in the Southern Ocean. *Polar Biology*, **31**, 809–816.

Waller, C.L., Barnes, D.K. & Convey, P. (2006) Ecological contrasts across an Antarctic land–sea interface. *Austral Ecology*, **31**, 656–666.

Waters, J.M. (2008) Driven by the West Wind Drift? A synthesis of southern temperate marine biogeography, with new directions for dispersalism. *Journal of Biogeography*, **35**, 417–427.

Waters, J.M., Fraser, C.I. & Hewitt, G.M. (2013) Founder takes all: density-dependent processes structure biodiversity. *Trends in Ecology and Evolution*, **28**, 78–85.

Wootton, J.T. (1991) Direct and indirect effects of nutrients on intertidal community structure: variable consequences of seabird guano. *Journal of Experimental Marine Biology and Ecology*, **151**, 139–153.

WoRMS Editorial Board (2015) World Register of Marine Species. Available at: //www.marinespecies.org at VLIZ (accessed 17 June 2015).

Wouters, B., Martin-Español, A., Helm, V., Flament, T., van Wessem, J.M., van den Ligtenberg, S.R., Broeke, M.R. & Bamber, J.L. (2015) Dynamic thinning of glaciers on the Southern Antarctic Peninsula. *Science*, **348**, 899–903.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 The references used to create the intertidal occurrence database.
Appendix S2 Counts of species, to order level, per region of the Antarctic and Sub-Antarctic.
Appendix S3 Significant ANOSIM and SIMPER results.

BIOSKETCHES

Huw Griffiths is a marine biogeographer with an interest in; large-scale biogeographical and ecological patterns in space–time, using model groups to investigate trends in distribution at high southern latitudes and utilizing large biological and physical databases to understand key processes in the Antarctic. He is chair of the SCAR (Scientific Committee

on Antarctic Research) scientific research programme AntEco (State of the Antarctic Ecosystem) and theme leader for the Spatial Ecology sector.

Cath Waller is a marine biologist at the University of Hull. Her doctoral research investigated the ecology of the Antarctic intertidal zone, the animals that live there and the adaptations they have developed in order to survive. She studies the ecology, biogeography and ecophysiology of intertidal species and is interested in the effects of environmental change on the Antarctic intertidal ecosystem and the potential for marine invasive species to colonize this habitat.

Editor: Jonathan Waters