The South Sandwich Islands – a community of meta-populations across all trophic levels.

Abstract

The South Sandwich Islands are a volcanic archipelago in the Southern Ocean that are remote and largely pristine, but experience high levels of natural disturbance, and pose interesting and challenging questions for conservation and management. The archipelago lies to the south of the oceanic Antarctic Polar Front, in the biological transition region between the sub-Antarctic and maritime Antarctic. They host the southern boundary for some sub-Antarctic communities and the northern boundary for some from the maritime Antarctic. Vertebrate communities are dominated by Chinstrap and Macaroni penguins in the north and Adélie penguins in the south. Terrestrial plant and animal communities are not so well differentiated. Instead, their composition and extent are more influenced by the distribution of geothermally-warmed ground, although the archipelago again hosts representatives of both sub- and maritime Antarctic origin. We review the current knowledge about the islands' biodiversity, the influence of contemporary change on the archipelago, and their regional importance to Southern Ocean species. We summarise likely threats to the archipelago's biodiversity, and pose questions that are important for developing effective management strategies particularly in the contexts of climate change, fishery exploitation and human visitation. We anticipate that, while climate change and fisheries will likely lead to a range of impacts on the islands' biota, introduced species are likely to be the most immediate and largest threat to ecosystems on land in the archipelago. Given the ephemeral nature of populations across all trophic levels, we suggest that the islands be managed as one unit rather than individually, and we recommend practical changes to risk assessment, permitting and to consider increasing the no take area in the existing Marine Protected Area to protect penguin foraging areas.

Key words:

Volcano; island biogeography, island conservation, terrestrial protected area, invasive species

Word count: 7808

Discovery, and human impact

The South Sandwich Islands were first discovery by Captain James Cook in 1775 on HMS *Resolution*, during his second circumnavigation expedition[1]. Cook first viewed Candlemas Island and progressed south to Saunders, Montagu, Bristol, Bellingshausen, Cook and Thule before heading north and east to South America[2]. After Cook, some of the islands may have been visited by sealers in 1816-1818[3].

Relatively low numbers of seals were taken, due to their low abundance and the small and inaccessible nature of their haul-out beaches. However, this may still have reduced local populations near to extinction. The northern three islands of the chain (Zavodovski, Visokoi, Leskov) were officially discovered substantially later by Bellingshausen in 1819[4]. These are collectively known as the Traversay Islands after the Marquis de Traversay, a French émigré who joined the Russian Navy.

Also of note was the visit of Benjamin Morell on board the sealing vessel *Wasp*, who likely visited the islands in 1823[5]. His descriptions of the islands and their fauna are broadly consistent, but many of his other claims remain disputed due to navigational[6] and biological inconsistencies[7]. Capt J Brown possibly carried out some sealing around Zavodovski in 1834[7,8], although with no reporting of numbers. Following these early voyages of discovery and exploration, the islands were largely ignored until some seal prospecting visits in the late 1870s, with 2000 skins reported in the three northern islands[9], and six ships taking 4000 skins in 1876-7. Sealers continued to visit the islands in 1877-78, 1880-81 and 1891-98 but took less than 500 skins, with no seals taken in 1880-81[10]. Thus, while we think of the South Sandwich Islands as relatively pristine, those islands that can support seals have been heavily exploited, and in light of the number of skins reported compared to current numbers, populations may not have yet fully recovered.

As far as is documented, Carl Anton Larson next visited with the *Undine* in 1908. He landed on most of the islands and made detailed observations and sketches of the islands. He inhaled toxic fumes on Zavodovski and that, coupled with the weather and poor anchor holding, gave him an unfavourable impression of the archipelago:

"November the 12th. The same bad weather as yesterday. "*Undine*" was obliged to lie drifting. Many times we were under the land, but on account of the high sea it was quite impossible to go on shore anywhere."

Larsen subsequently focussed his commercial interests and activities on land-based whaling stations on South Georgia, and the islands were once again left ignored until the scientific era was heralded by RRS *Discovery II* in 1931. This expedition examined most of the islands, but was primarily focussed on whales and the marine ecosystem in their vicinity[11]. In 1956, Argentina built and operated briefly the summer-only base *Teniente Esquivel* on Hewison Point, Thule Island. This was evacuated in 1956 due to an eruption of Mount Holdgate (subsequently named) on Cook Island across Douglas Strait[12].

In 1964, the second major scientific expedition to the archipelago took place, in the form of a Royal Society sponsored expedition supported by HMS *Protector*, on this occasion with a greater focus on the islands themselves, with landings and surveys completed on parts of most of the islands[13].

Following this, and with increasing tensions over sovereignty, Argentina built and operated *Corbeta Uruguay* Station in 1976, again on Thule Island, which was discovered, protested and negotiated over. The station remained controversial and in operation until 1982, when it was destroyed at the end of the Falklands Conflict by the UK Royal Navy[14]. Although a small refuge hut remained at the location after this (now collapsed), the islands have remained uninhabited since, but wreckage and pollution remain from this station.

The islands remain seldom visited for any reason, but tourist vessels have landed personnel occasionally on Zavodovski, Candlemas, Saunders and Thule, both by boat and helicopter. The South African National Antarctic Programme also operates a remote unmanned meteorological station on Zavodovski, which is accessed annually by helicopter by their Antarctic support vessel en route to/from SANAE station on the Antarctic continent. Post-1964, three recent scientific expeditions have surveyed all or parts of the archipelago. These are HMS *Endurance*/RRS *James Clarke Ross* and a party of geologists and biologists from the British Antarctic Survey in early 1997[15-18], Jerome Poncet in the SY *Damien II* also in early 1997[15], and then a team on board SY *Golden Fleece* in 2011[19,20]. The difficulty of reaching and operating within the islands largely protects them from human landing and disturbance, and it is notable the HMS *Protector* and HMS *Endurance* expeditions utilised helicopter support to achieve greater ground coverage. Our knowledge of the invertebrate fauna and flora of the islands primarily derives from specimens and data obtained during these two expeditions.

In 2012, GSGSSI created what was then the world's largest marine protected area, extending out to the 200 nautical mile limit surrounding both South Georgia and the South Sandwich Islands[21], limited to the south by the 60 degree latitude parallel, which defines the limit of the Antarctic Treaty System. To bring similar scrutiny to the terrestrial environment, in 2017 the Government of South Georgia and the South Sandwich Islands (GSGSSI) initiated a review of terrestrial protection within their jurisdiction. It is therefore timely to reconsider the islands in terms of their biodiversity and ecosystems and as wilderness areas, identify the threats to them, both natural and anthropogenic, and recommend appropriate management approaches. Recognising that there is a separate Marine Protected Area review underway, we also highlight the extent of influence of the terrestrial (mostly breeding vertebrate) component on the surrounding marine environment.

Geology and Cryology

The South Sandwich Islands comprise a volcanic island chain of 11 islands towards the western edge of the Scotia Plate[13,22]. The islands form as the South American plate subducts under the East Scotia plate and melts, venting occasionally[23]. Geologically, the existing individual islands are relatively recent, but a succession of such islands is likely to be a permanent feature of the subduction zone and

venting, and the exact nature and composition of the islands is likely to be ever-changing. While at present there are 11 islands, further seamounts such as Protector Shoal north of Zavodovski reach close to the surface and have the potential to emerge as islands. To the east of the island chain is the South Sandwich Trench, which reaches depths commonly around 6000 m, but exceeding 8000 m locally in Meteor Deep[22,24,25].

[Figure 2 near here]

The islands lie to the north-east of the Weddell Sea which, as part of the Weddell Sea Gyre, pumps sea ice out into the Scotia Sea, where it is pushed east by winds and the Antarctic Circumpolar Current. The South Sandwich Islands often represent the most northerly extent of Antarctic sea ice[26].

Flora

For the purposes of reviewing the community of terrestrial organisms throughout the South Sandwich Islands (Table 1, 2), we consider any vegetation and wildlife above the tideline as 'terrestrial', although Pugh et al.[27] include intertidal and supralittoral species in their regional study. Two surveys of the flora of the South Sandwich Islands have been undertaken; that supported by HMS *Protector* in early 1964[13], and that supported by HMS *Endurance* and RSS *James Clark Ross*, combined with a four week field camp on Candlemas Island, in early 1997[17]. Combining these two surveys shows that the archipelago has substantial ice-free areas that are suitable for vegetation and that there is a relatively diverse flora. The currently-documented flora comprises one phanerogam (flowering plant), 38 mosses, 11 liverworts, five basidiomycete fungi, 41 lichenised fungi and 16 diatoms with, additionally, several taxa identified only to genus[17]. Major elements of the moss and liverwort floras are composed of South American taxa (32% and 73%, respectively), with a further 45% of mosses having bipolar or cosmopolitan distributions. These two groups show low levels of Antarctic endemicity (11% and 18%, respectively), as is typical of Antarctic mosses generally. One important caveat to these figures is that this diversity is based on traditional morphological taxonomy; recent studies of Antarctic mosses[28] show considerable molecular divergence between Antarctic regions, and the concept of 'cryptic speciation' is yet to be examined either generally in Antarctic bryophytes, or specifically in the South Sandwich Islands flora; it may well be the case that they show divergence from known Antarctic mosses[28-30], over timescales of 1-5 MY[28]. In contrast, 52% of the lichens recorded and 80% of the basidiomycete fungi are currently thought to be endemic to the Antarctic, with these lichens only otherwise known from locations further south in the maritime or continental Antarctic[31,32]. This may suggest a refugial role for the South Sandwich Islands over the last 1-3 million years of their existence[26]. A further 36% of lichens are bipolar or cosmopolitan, with only 5% of South American origin. In the light of the apparent lack of endemism and the ephemeral nature of volcanic soils, it

seems appropriate to consider the South Sandwich Islands as being of regional, but not global importance for these taxa.

The flora of the South Sandwich Islands is clearly derived from those of other Antarctic zones. The flora of unheated ground is closely related to that of the maritime Antarctic, although with a more limited number of species represented[17,28]. That of heated ground, a striking feature of the vegetation of particularly Bellingshausen and Candlemas Islands, contains both maritime and sub-Antarctic and some lower latitude elements, confirming the importance of geothermal heating for successful colonisation of the latter group[17]. A few specific genera, particularly *Campylopus*, are often associated with geothermal activity elsewhere, such as Hawaii[33], Iceland[34] and New Zealand[35]. The occurrence of several species generally well distributed in the maritime Antarctic only on heated ground in the archipelago confirms the extreme severity of the archipelago's climate in comparison with well-studied sites much further south in this biogeographical zone[36] and may reflect the relatively cold maritime climate, with high frequency and extent of winter sea ice (Figure 1).

The greatest bryophyte richness is associated with geothermally influenced ground. Of 35 moss and 11 liverwort species recorded, only four mosses were never associated with heated ground, while eight of the liverworts and 50% of the mosses were found only on actively or recently heated ground. Several species occur in distinct and often concentric 'zones' around fumaroles. Maximum temperatures recorded within the upper 0.5 cm of the vegetation surface were 40 - 47 °C, with only *Campylopus introflexus* tolerating such temperatures[36]. Maximum temperatures 2.5 or 5 cm below the vegetation surface of this moss reached 75 °C. Other bryophytes regularly present in zoned vegetation included the mosses *Dicranella hookeri*, *Sanionia georgicouncinata*, *Pohlia nutans* and *Notoligotrichum trichodon*, and the liverworts *Cryptochila grandiflora* and *Marchantia berteroana*. Surface temperatures of 25 - 35 °C and subsurface temperatures of 50 - 60 °C were recorded in these species. The distribution of plant communities around geothermally influenced ground demonstrates the ephemeral nature of these communities, as it is well-known that fumaroles and other heated areas are transient on scales of months to years or decades, as well as varying in their temperature on much shorter timescales[17,37]. It therefore seems likely that there are metapopulations of the species occurring in these communities colonising on a local scale.

These exceptional plant communities illustrate the transport of viable propagules into the Antarctic. Individually ephemeral in nature, temporally overlapping existence of geothermal habitats in the longer term on islands along the Scotia Arc may have provided refugia during periods of glacial expansion, facilitating subsequent recolonization of Antarctic terrestrial habitats[17,38].

Evidence of change and threats to flora

Currently, is no evidence of change in any community, but this is simply due to data deficiency; there have been two baseline surveys and no monitoring. Convey et al. [17] suggest expansion of the grass population and the development of an unheated moss bank on Candlemas. In light of the recent eruptions on Zavodovski and Saunders Islands, there is good opportunity for comparison post-eruption. It should be noted in conservation and management plans that there is likely to be relatively frequent disturbance on some or all of the islands due to eruption and also lesser volcanic events.

There are threats due to (infrequent) human presence on the islands, but the archipelago's greatest protective asset is its isolation and the extreme difficulty of landing on many of the islands. Threats to flora in particular come from trampling – Antarctic mosses have been shown to be particularly vulnerable to trampling and any physical damage. Other than the grass *Deschampsia antarctica*, none of these plant communities have roots and those on heated ground are very sensitive to temperature – any slight compression can take the living part above its maximum survivable temperature. In light of this, all care should be taken to avoid walking on vegetation and advice to this end should be included in issued permits.

Second to physical threats is that of invasive species. Polar resident species of both flora and fauna tend to be very well adapted to extreme and highly seasonal polar conditions. The flipside of this is that they tend to be inherently weak competitors if faced with a challenge[39], or for example under climate change scenarios. Many of the sub-Antarctic Islands have been colonised by invasive species[40] and South Georgia has already had 76 invasive plant species, of which 41 are thought to still be present[41]. Those species that have already been able to establish in South Georgia may be strong candidates establishment in the South Sandwich Islands as they are already south of the Polar Front. Moreover, the potential for establishment of introduced plant species is likely to be particularly acute as plants may survive on warmed ground much further south than they otherwise could. Invasive species are one of the largest agents of global ecological change[42,43] and one of the largest threats to the South Sandwich Islands, and should be aggressively tackled[44,45].

Invasive plants and also invertebrates could arrive at South Georgia and the South Sandwich Islands from ports of origin entrained in cargo, equipment or clothing of ships' crew, national and tourist operator staff, scientists and tourists[42,46]. GSGSSI[47] and IAATO guidelines are stringent about biosecurity prior to first landing south of the Polar Front, but need to be equally rigorously applied in movements between landing sites, as propagules have frequently been detected between sites[42,48]. Currently, all vessels approaching the South Sandwich Islands require clearance from the GSGSSI administrative centre at King Edward Point in East Cumberland Bay on South Georgia. This is itself a

bay with the highest number and abundance of invasive floral and invertebrate species on South Georgia (31 of 41 invasive plant species are present in Cumberland Bay)[41], making the island itself a likely source of further regional invasions of plants, invertebrates, fungi and other microbes. To reduce some of these risks, GSGSSI might consider permitting vessels to go through biosecurity checks at the port of departure, such as in Stanley, and to land directly on SSI without first passing through South Georgia (although this then requires extra biosecurity at departure ports), or practical mitigation such as a ban on Velcro on outer clothing (although noting that, once entrapped in Velcro, propagules actually have a lower chance of being deposited[49]). The South Georgia Government Biosecurity Handbook 2017-18 states "for particularly high-risk projects (such as some construction work, expeditions, science/monitoring in sensitive areas) a bespoke biosecurity plan is necessary"[50]. We would argue that this is the case for any visitor to SSI and that permit applicants should put together a tailored risk plan based on their origin and objectives.

Invertebrate fauna

Terrestrial fauna (Table 2) are also limited to ice-free areas and comprise 29 free-living micro-arthropod species (nine Collembola and 20 Acari), six tardigrades and two unidentified enchytraeid worms[16,51]. No studies have addressed other members of the meiofauna typical of Antarctic terrestrial habitats, particularly the nematode worms and rotifers, although these undoubtedly occur in the archipelago. It is possible that at least one of the unidentified enchytraeid species may be the same as one described from South Georgia and Signy Island in the South Orkneys[52]. A further eight parasitic and sublittoral Acari are recorded in the literature[16]. Freshwater habitats are very restricted in the archipelago and no freshwater fauna were located in either the 1964 or 1997 surveys. Supralittoral pools on an exposed low headland at Fryer Point, Bristol Island contained the marine isopod *Cassidinopsis maculata*. There are no endemic taxa and no shoreline invertebrates other than the supralittoral *Archisotoma brucei* (Collembola) and the two Enchytraeidae. Diversity on individual islands is, in part, a function of available ice-free ground area. The majority of dominant species throughout the archipelago, *Cryptopygus antarcticus* (Collembola), *Nanorchestes nivalis*, *Eupodes minutus*, *Alaskozetes antarcticus* and *Halozetes belgicae* (Acarina), occur on other maritime Antarctic islands, while *Ayersacarus tilbrooki* (Acarina) is sub-Antarctic. Few (one to three) individuals of several other sub-Antarctic species were recorded by either the 1964 or 1997 expeditions, but only *Pilellus rykei* (Acarina) was reported by both. At present we are unable to differentiate whether such records indicate ephemeral colonisation and then extinction, or simply that survey work carried out to date is insufficient to capture the full terrestrial invertebrate diversity of the archipelago. None of the sub-Antarctic species thought to be associated with geothermally warmed ground in 1964[13] were confirmed in 1997[17], despite extensive sampling of the same sites.

Cryptopygus caecus (now known as *Mucrosomia caeca* (Wahlgren)), now widespread on Candlemas Island, is a solitary exception to this generalization – it is a species common on South Georgia, and is also associated with geothermal activity on the maritime Antarctic Deception Island (South Shetland Islands)[53]. Work on Deception Island has shown rates of colonisation and recolonisation[37,54,55] that add to the possibility of insect metapopulations across the archipelago, possibly assisted by avian transfer between islands[56].

Vertebrate populations

A complete list of vertebrates recorded in the archipelago is included in Table 3, primarily derived from the two detailed surveys[15,19], with additional information from early visits[13]. The dominant biota are penguin species, including Chinstrap (*Pygoscelis antarctica*) and Macaroni penguins (*Eudyptes chrysolophus*) in the northern islands, and Chinstrap and Adélie penguins (*Pygoscelis adeliae*) in the southern islands. Gentoo penguins (*Pygoscelis papua*) exist as both small colonies and isolated individuals throughout the archipelago. Small numbers of King penguins (*Aptenodytes patagonicus*) are found throughout, with a number of reports of possibly incubating birds particularly on Zavodovski Island[15] but no confirmed records of chicks. There is a broad distinction between more northerly assemblages (as typified on Candlemas Island) and more southerly species assemblages found from Saunders Island southwards. Despite their hostile weather, isolation and infrequent visits, there are relatively good population estimates for many of the species, with the caveat that the recent eruptions of Zavodovski, Saunders and Bristol Islands may have impacted local populations dramatically (highlighted in Table 3).

Collectively, the archipelago has half of the total global breeding population of Chinstrap penguins[19,57] approximately 1.3 million of which form one super-colony on Zavadovski[19], likely the world's largest bird colony. Estimates of penguin numbers come initially from Baker[13], then with more precision from Convey et al.[15], refined in 2011 by the SY *Golden Fleece* expedition[19]. With caveats, the most recent survey suggests that populations are largely stable[19], in contrast with anthropogenically-forced populations elsewhere in the Scotia Arc[58] and Antarctic Peninsula[59-62]. Recent eruptions of Candlemas and Bristol in 1953[13], and of Zavodovski and Bristol in 2015, suggest that many of the nesting areas of the islands may be ephemeral. Eruptions of ash cloud and gas are likely to make the nesting surfaces of penguins temporarily uninhabitable, as suggested with volcanism in the South Shetland Islands[63]. However, the recent 2015 eruption remains ambiguous in its timing to ascertain whether penguins were caught on the nest, or if the majority were at sea in their pre-moult foraging trip. There is evidence of similar historic eruptions causing mass mortality on Zavodovski and Saunders Islands, similar to those recently documented in historic deposits on Ardley Island[63].

Population sizes of penguins on the South Sandwich Islands are likely to represent an equilibrium of colonisation or population growth versus intermittent if drastic disturbance. Recent genetic work shows that penguins can be genetically differentiated over smaller distances than those between the South Sandwich Islands and next nearest land[64], but also that a range of population structures have been detected in penguins[20,65-68] and other seabirds[69-71]. While no Gentoo penguins from SSI have been included in genetic studies, it is likely that they are genetically close to South Georgia, but exchanging very few migrants between these archipelagos per generation[64]. In contrast, genetic evidence suggest relatively high connectivity in Chinstrap penguins between the SSI, the South Orkney Islands and the Antarctic Peninsula[20], and more resolved data also suggest connectivity between Bouvet Island (Clucas, pers comm), SSI and the rest of the maritime Antarctic. Genetic evidence of linkage is backed up by individual tracks[72,73] and stable isotope studies[74]. Unpublished data on Macaroni penguins suggests weak differentiation over South Georgia, which (due to the separation distances) likely means that populations on the SSI are genetically very weakly differentiated from each other (and therefore could be treated as one population) and likely only weakly differentiated from those on South Georgia.

Breeding phenology cameras installed on Saunders Island suggest that Chinstrap penguins there breed later than on the Antarctic Peninsula, contrasting with an observation of slightly earlier breeding in the 2011 RV *Golden Fleece* expedition. It is plausible that breeding phenology is highly dependent on the timing of sea ice retreat around the islands (see Fig. 2 for annual variation in sea ice extent around the archipelago over the last decade), which may be more variable than in the rest of the maritime Antarctic. Krill supply is likely to be one of the greatest uncertainties in breeding success, and is hard to assess. No data exist documenting the frequency of poor krill years on the SSI, a phenomenon that is known affect reproductive success in South Georgia Antarctic fur seals[75-77] and penguins[78], penguins in the South Orkney Islands[79,80] and the western Antarctic Peninsula[81-84] and other seabirds[85].

Flying seabirds are present in lower numbers than penguins (Table 3), but the islands are likely to host regionally important numbers of Snow Petrel (*Pagodroma nivea*), Southern Fulmar (*Fulmarus glacialoides*), Wilson's storm petrel (*Oceanites oceanicus*) and cape petrel (*Daption capense*). The genetic isolation of these flying birds is unknown, but likely to be less than the differentiation exhibited by penguins because of dispersal during winter and wider mixing during non-breeding[70,86]. The SSI are, surprisingly, free of Snowy Sheathbill (*Chionis albus*), a scavenger and egg predator that is characteristic of large penguin populations elsewhere on the Antarctic Peninsula and Scotia Arc, including South Georgia.

The seabirds recorded primarily nest on cliffs, with notable exceptions of some populations of shag, Brown Skua and giant petrels nesting on open, flat ground. It is possible that cliffs are more stable, long term features that are less prone to volcanic disturbance than are the locations of penguin colonies, as it is harder for ash to settle on cliffs and many of the important stacks are offshore from the main islands. Moreover, flying seabirds may find it easier to abandon nest sites than penguins undergoing their catastrophic moult.

In contrast to South Georgia, the SSI are rat–free, and indeed no invasive species of vertebrate, invertebrate or plant have ever been recorded. It is not clear whether any were ever introduced to the islands – although intuitively this seems likely as rats were endemic to sealing era vessels that visited the islands - but, as with locations further south in the maritime Antarctic there is likely insufficient food available for them over winter between bird breeding seasons, so it is unclear whether at present they would establish successfully if introduced[40].

The lack of historic visitation, and the relatively low numbers of fur and elephant seals, mean that the islands were not exploited to the same level as South Georgia, and may even have provided some of the migrants that recolonized mainland South Georgia post-sealing effort. Relatively small numbers of Antarctic fur seals (*Arctocephalus gazella*) breed on the northern islands of Zavodovski, Visokoi, Candlemas and Saunders. Due to small beaches, these are likely to be at or near carrying capacity other than on Saunders Island. There is very little evidence of genetic structure across the Southern Ocean fur seal population[87], although so far the South Sandwich Islands have not been sampled or sequenced. Contrasting evidence suggests that, post sealing, variance is likely to be low[87] with observations of high natal site fidelity[88], likely to give rise to population structure.

As with penguins, there is a divide between communities north and south of Candlemas/Vindication, where the mean November sea ice extent may limit these maritime or sub-Antarctic breeders (Table 3, Figure 2). Southern elephant seals (*Mirounga leonina*) are present throughout the islands on beaches, but have not been observed breeding. Given breeding times in South Georgia, it is likely that beaches are not free of sea ice at suitable times to breed and that the individuals observed are non-breeding or resting during post-breeding foraging trips. Similarly, Weddell (*Leptonychotes weddelli*), crabeater (*Lobodon carcinophagus*) and leopard seals (*Hydruga leptonyx*) are seen occasionally throughout the archipelago. It is entirely possible that these may breed in low numbers at times of the year when the islands are not surveyed. In particular, crabeater and leopard seals are hard to survey as they breed on sea ice, while Weddell seals utilise land fast ice.

The SSI include either the northern or southern distributional limits of several species. Climate change could therefore alter the distribution and relative abundance of ‘northern’ and ‘southern’ specialists.

The biggest source of variance and of change is likely to be through the timing and extent of sea ice. All islands are frequently surrounded by sea ice during winter, but there is a distinction between the timing of when islands become ice free north and south of Candlemas Island (Figure 2), which reflects the abrupt change from sub-Antarctic/maritime specialists to ice tolerant/Antarctic specialists.

There is currently a small toothfish fishery around the South Sandwich Islands in the SGSSI maritime zone north of 60°S. At present there is negligible krill fishing effort, and there is a complete no take zone of 3 nm and a pelagic no take zone of 12 nm around every island. The threat from overfishing of krill is currently low, but significant increases in this fishery could be very damaging. In particular, as regional whale populations recover there is likely to be less krill surplus for fishing[83], especially at a local scale.

In context of the current GSGSSI MPA review, it should be noted that Chinstrap, Macaroni and Adélie penguins, and Antarctic fur seals, are all offshore pelagic predators, so if the krill fishery were to develop, the 12 nm buffer is likely to be insufficient to afford protection to such a high density of predators. No tracking studies have been conducted for these species on the South Sandwich Islands, but elsewhere breeding Chinstrap penguins have been shown to have large ranges, between 26 and 35 nm offshore[80,89-92], while Macaroni penguins have larger offshore ranges of 40 -100 nm[93-96], Adélie penguins have intermediate foraging ranges of 10-50[80], and Gentoos the smallest of 15 nm offshore[80]. In light of this, the precautionary no take zones around the South Sandwich Islands of 3-12 nm would seem to be inadequate and there is a strong argument for extending these to 40-80 nm offshore based on foraging ranges, given the globally important populations of chinstrap penguins and their footprint of dependency on the surrounding ocean We note that such a precautionary expansion of a buffer zone would also apply to South Georgia.

Conclusions

The South Sandwich Islands contain both globally and regionally important populations of flora and fauna, and host what is likely to be the largest bird colony in the world. Likely threats to the islands from climate change are moderate, and the threat from invasive species is hard to assess in terms of risk, but likely high impact if any invasions occurred. The possibility of a plant or invertebrate invasive species taking hold can be reduced by the effective application of strict biosecurity protocols and, possibly, by applying more stringent rules relating to successive landings on the South Georgia mainland and the SSI. Unmitigated, terrestrial invasions are likely to be one of the greatest threats to the archipelago's biota.

As discussed above (particularly with regard to biosecurity), any activities on the islands should be risk assessed in terms of how impactful these may be on habitats as a whole, both for the risk of invasion,

but also disturbance. We conclude that most of the biota on these islands can be treated as meta-populations across the archipelago, particularly in environmental risk assessments for permits. Finally, we must recognise that there are practical limits to conservation; this exceptional archipelago contains naturally ephemeral communities in part due to volcanic activity. It is this activity that is likely to drive natural cycles in abundance on the islands.

Cited Literature

1 Cook, J., Furneaux, T., Hodges, W. & Pringle, J. *A voyage towards the South Pole, and round the world. Performed in His Majesty's ships the Resolution and Adventure, in the years 1772, 1773, 1774, and 1775*. The 2d edn, (W. Strahan and T. Cadell, 1777).

2 Baker, C. S. *et al.* Estimating the number of whales entering trade using DNA profiling and capture-recapture analysis of market products. *Molecular Ecology* **16**, 2617-2626, doi:10.1111/j.1365-294X.2007.03317.x (2007).

3 Headland, R. *The Island of South Georgia*. (Cambridge : Cambridge University Press, 1984 (1992 [printing]), 1992).

4 Headland, R. & Roberts, B. B. *Chronological list of Antarctic expeditions and related historical events*. (Cambridge University Press, 1989).

5 Morrell, B. *A Narrative of four voyages to the South Sea, North and South Pacific Ocean, Chinese Sea, Ethiopic and Southern Atlantic Ocean, Indian and Antarctic Ocean, from ... 1822 to 1831. ... To which is prefixed a brief sketch of the author's early life*. (New York, 1832).

6 Bertrand, K. J. *Americans in Antarctica, 1775-1948*. (American Geographical Society, 1971).

7 Holdgate, M. W. & Baker, P. E. *The South Sandwich Islands: I. General description*. Vol. 91 (British Antarctic Survey, 1979).

8 Fanning, E. *Voyages round the world : with selected sketches of voyages to the South Seas, North and South Pacific Oceans, China, etc., performed under the command and agency of the author : also, information relating to important late discoveries; between the years 1792 and 1832, together with the report of the commander of the first American exploring expedition, patronised by the United States government, in the brigs Seraph and Annawan, to the Southern Hemisphere*. (Collins & Hannay, 1833).

9 Jordan, D. S. *The fur seals and fur-seal islands of the North Pacific Ocean*. (G.P.O, 1898).

10 Jordan, D. S. *The fur seals and fur-seal islands of the North Pacific Ocean*. (G.P.O, 1899).

11 Kemp, S., Nelson, Nelson, A. L. & Tyrrell, G. W. *The South Sandwich Islands ... With a report on Rock Specimens by G. W. Tyrrell*. (1931, 1931).

12 Canclini, A. (Zagier & Urruty, 2009).

13 Baker, P. E. *et al.* Survey of South Sandwich Islands. *Nature* **203**, 691-& (1964).

14 Perkins, R. *Operation Paraquat : the battle for South Georgia*. (Picton, 1986).

15 Convey, P., Morton, A. & Poncet, J. Survey of marine birds and mammals of the South Sandwich Islands. *Polar Rec* **35**, 107-124 (1997).

16 Convey, P., Greenslade, P. & Pugh, P. J. A. The terrestrial micro-arthropod fauna of the South Sandwich Islands. *J Nat Hist* **34**, 597-609, doi:Doi 10.1080/002229300299462 (2000).

17 Convey, P., Smith, R. I. L., Hodgson, D. A. & Peat, H. J. The flora of the South Sandwich Islands, with particular reference to the influence of geothermal heating. *J Biogeogr* **27**, 1279-1295, doi:DOI 10.1046/j.1365-2699.2000.00512.x (2000).

18 Convey, P. *Biological survey of the South Sandwich Islands, 1996/7 field season* (British Antarctic Suvey, Cambridge, 1997).

19 Lynch, H. J. *et al.* In stark contrast to widespread declines along the Scotia Arc, a survey of the South Sandwich Islands finds a robust seabird community. *Polar Biol* **39**, 1615-1625, doi:10.1007/s00300-015-1886-6 (2016).

20 Freer, J. *et al.* Limited genetic differentiation among chinstrap penguin (Pygoscelis antarctica) colonies in the Scotia Arc and Western Antarctic Peninsula. *Polar Biol*, 1-10, doi:10.1007/s00300-015-1711-2 (2015).
21 Trathan, P. N. *et al.* in *Advances in marine biology* Vol. 69 15-78 (Elsevier, 2014).
22 Leat, P. T. *et al.* Bathymetry and geological setting of the South Sandwich Islands volcanic arc. *Antarctic Science* **28**, 293-303, doi:10.1017/S0954102016000043 (2016).
23 Pearce, J. A., Baker, P. E., Harvey, P. K. & Luff, I. W. Geochemical Evidence for Subduction Fluxes, Mantle Melting and Fractional Crystallization beneath the South Sandwich-Island Arc. *J Petrol* **36**, 1073-1109 (1995).
24 Frankel, A. & Mccann, W. South Sandwich Arc Seismicity - Consequences of a Ridge-Trench Collision. *Eos T Am Geophys Un* **58**, 509-509 (1977).
25 Vanneste, L. E., Larter, R. D. & Smythe, D. K. Slice of intraoceanic arc: Insights from the first multichannel seismic reflection profile across the South Sandwich island arc. *Geology* **30**, 819-822, doi:Doi 10.1130/0091-7613(2002)030<0819:Soiaif>2.0.Co;2 (2002).
26 Renner, A. H. H., Heywood, K. J. & Thorpe, S. E. Validation of three global ocean models in the Weddell Sea. *Ocean Modelling* **30**, 1-15, doi:DOI 10.1016/j.ocemod.2009.05.007 (2009).
27 Pugh, P. & Convey, P. Surviving out in the cold: Antarctic endemic invertebrates and their refugia. *J Biogeogr* **35**, 2176-2186 (2008).
28 Biersma, E. M. *et al.* Global biogeographic patterns in bipolar moss species. *Royal Society open science* **4**, 170147, doi:10.1098/rsos.170147 (2017).
29 Cannone, N. *et al.* Moss survival through in situ cryptobiosis after six centuries of glacier burial. *Sci Rep-Uk* **7**, doi:Artn 4438
10.1038/S41598-017-04848-6 (2017).
30 Cannone, N., Fratte, M. D., Convey, P., Worland, M. R. & Guglielmin, M. Ecology of moss banks on Signy Island (maritime Antarctic). *Bot J Linn Soc* **184**, 518-533, doi:10.1093/botlinnean/box040 (2017).
31 Øvstedal, D. O. & Smith, R. I. L. *Lichens of Antarctica and South Georgia: a guide to their identification and ecology*. (Cambridge University Press, 2001).
32 Casanovas, P., Lynch, H. J. & Fagan, W. F. Multi-scale patterns of moss and lichen richness on the Antarctic Peninsula. *Ecography* **36**, 209-219 (2013).
33 Kappen, L. & Smith, C. W. Heat tolerance of two Cladonia species and Campylopus praemorsus in a hot steam vent area of Hawaii. *Oecologia* **47**, 184-189, doi:10.1007/bf00346818 (1980).
34 Elmarsdottir, A., Ingimarsdottir, M., Hansen, Í. R., Ólafsson, J. S. & Olafsson, E. Vegetation and invertebrates in three geothermal areas in Iceland. *000599234* (2003).
35 Smale, M. C., Wiser, S. K., Bergin, M. J. & Fitzgerald, N. B. A classification of the geothermal vegetation of the Taupō Volcanic Zone, New Zealand. *Journal of the Royal Society of New Zealand* **48**, 21-38, doi:10.1080/03036758.2017.1322619 (2018).
36 Convey, P. & Lewis, S. R. I. Geothermal bryophyte habitats in the South Sandwich Islands, maritime Antarctic. *J Veg Sci* **17**, 529-538, doi:DOI 10.1111/j.1654-1103.2006.tb02474.x (2006).
37 Smith, R. I. L. The bryophyte flora of geothermal habitats on Deception Island, Antarctica. *J Hattori Bot Lab*, 233-248 (2005).
38 Fraser, C. I., Terauds, A., Smellie, J., Convey, P. & Chown, S. L. Geothermal activity helps life survive glacial cycles. *Proceedings of the National Academy of Sciences* **111**, 5634-5639 (2014).
39 Convey, P. The influence of environmental characteristics on life history attributes of Antarctic terrestrial biota. *Biological Reviews* **71**, 191-225 (1996).
40 Convey, P. & Lebouvier, M. in *Papers and proceedings of the royal society of Tasmania.* 33-44.
41 Upson, R. *et al. Field Guide to the Introduced Flora of South Georgia*. (Kew Publishing, 2017).

42 Chown, S. L. *et al.* Continent-wide risk assessment for the establishment of nonindigenous species in Antarctica. *Proceedings of the National Academy of Sciences* **109**, 4938-4943 (2012).

43 Frenot, Y. *et al.* Biological invasions in the Antarctic: extent, impacts and implications. *Biological reviews* **80**, 45-72 (2005).

44 Baker, A. M., Hughes, J. M., Dean, J. C. & Bunn, S. E. Mitochondrial DNA reveals phylogenetic structuring and cryptic diversity in Australian freshwater macroinvertebrate assemblages. *Marine and Freshwater Research* **55**, 629-640, doi:10.1071/MF04050 (2004).

45 Hughes, K. A., Pertierra, L. R., Molina-Montenegro, M. A. & Convey, P. Biological invasions in terrestrial Antarctica: what is the current status and can we respond? *Biodivers Conserv* **24**, 1031-1055 (2015).

46 Huiskes, A. H. *et al.* Aliens in Antarctica: assessing transfer of plant propagules by human visitors to reduce invasion risk. *Biol Conserv* **171**, 278-284 (2014).

47 (Government of South Georgia & the South Sandwich Islands, http://www.gov.gs/docsarchive/Environment/Biosecurity/Biosecurity%20Handbook_2017-2018_FINAL.pdf, 2017).

48 Cowan, D. A. *et al.* Non-indigenous microorganisms in the Antarctic: assessing the risks. *Trends in microbiology* **19**, 540-548 (2011).

49 Lee, J. E. & Chown, S. L. Breaching the dispersal barrier to invasion: quantification and management. *Ecol Appl* **19**, 1944-1959, doi:Doi 10.1890/08-2157.1 (2009).

50 GSGSSI. (ed Government of South Georgia and the South Sandwich Islands) (2017).

51 Mcinnes, S. J. & Convey, P. Tardigrade fauna of the South Sandwich Islands, maritime Antarctic. *Zootaxa*, 43-49 (2005).

52 Dózsa-Farkas, K. & Convey, P. Christensenia, a new terrestrial enchytraeid genus from Antarctica. *Polar Biol* **17**, 482-486 (1997).

53 Greenslade, P., Potapov, M., Russell, D. & Convey, P. Global Collembola on Deception Island. *Journal of Insect Science* **12**, 1-16 (2012).

54 Smith, R. I. L. The thermophilic bryoflora of Deception Island: unique plant communities as a criterion for designating an Antarctic Specially Protected Area. *Antarctic Science* **17**, 17-27, doi:Doi 10.1017/S0954102005002385 (2005).

55 Smith, R. I. L. Colonization and Recovery by Cryptogams Following Recent Volcanic Activity on Deception Island, South Shetland Islands. *Brit Antarct Surv B*, 25-51 (1984).

56 Greenslade, P. & Convey, P. Exotic Collembola on subantarctic islands: pathways, origins and biology. *Biological Invasions* **14**, 405-417 (2012).

57 Lynch, H. J. & LaRue, M. A. First global census of the Adelie Penguin (vol 131, pg 457, 2014). *Auk* **133**, 236-236, doi:10.1642/Auk-15-231.1 (2016).

58 Forcada, J. & Trathan, P. N. Penguin responses to climate change in the Southern Ocean. *Global Change Biol* **15**, 1618-1630, doi:10.1111/j.1365-2486.2009.01909.x (2009).

59 Ducklow, H. W. *et al.* Marine pelagic ecosystems: The West Antarctic Peninsula. *Philos T R Soc B* **362**, 67-94, doi:DOI 10.1098/rstb.2006.1955 (2007).

60 Fraser, W. R. & Hofmann, E. E. A predator's perspective on causal links between climate change, physical forcing and ecosystem. *Mar Ecol Prog Ser* **265**, 1-15 (2003).

61 Lynch, H. J. & Larue, M. A. First global census of the Adelie Penguin. *Auk* **131**, 457-466, doi:10.1642/Auk-14-31.1 (2014).

62 Lynch, H. J., Naveen, R., Trathan, P. N. & Fagan, W. F. Spatially integrated assessment reveals widespread changes in penguin populations on the Antarctic Peninsula. *Ecology* **93**, 1367-1377 (2012).

63 Roberts, S. J. *et al.* Past penguin colony responses to explosive volcanism on the Antarctic Peninsula. *Nature communications* **8**, 14914, doi:10.1038/ncomms14914 (2017).

64 Levy, H. *et al.* Population structure and phylogeography of the Gentoo Penguin (*Pygoscelis papua*) across the Scotia Arc. *Ecology and evolution*, doi:10.1002/ece3.1929 (2016).

65 Clucas, G. V. *et al.* A reversal of fortunes: climate change 'winners' and 'losers' in Antarctic Peninsula penguins. *Sci. Rep.* **4**, doi:10.1038/srep05024 (2014).
66 Clucas, G. V. *et al.* Dispersal in the sub-Antarctic: king penguins show remarkably little population genetic differentiation across their range. *Bmc Evol Biol* **16**, doi:Artn 211 10.1186/S12862-016-0784-Z (2016).
67 Younger, J. L. *et al.* The challenges of detecting subtle population structure and its importance for the conservation of emperor penguins. *Molecular Ecology* **26**, 3883-3897, doi:10.1111/mec.14172 (2017).
68 Younger, J. L. *et al.* Too much of a good thing: sea ice extent may have forced emperor penguins into refugia during the last glacial maximum. *Global Change Biol*, n/a-n/a, doi:10.1111/gcb.12882 (2015).
69 Friesen, V. L. Population genetics and the spatial scale of conservation of colonial waterbirds. *Colon Waterbird* **20**, 353-368 (1997).
70 Friesen, V. L. Speciation in seabirds: why are there so many species...and why aren't there more? *J Ornithol* **156**, S27-S39, doi:10.1007/s10336-015-1235-0 (2015).
71 Rexer-Huber, K. *White-chinned petrel distribution, abundance and connectivity have circumpolar conservation implications*, University of Otago, (2017).
72 Biuw, M. *et al.* Long-range migration of a chinstrap penguin from Bouvetøya to Montagu Island, South Sandwich Islands. *Antarctic Science* **22**, 157, doi:10.1017/s0954102009990605 (2009).
73 Trivelpiece, W. Z., Buckelew, S., Reiss, C. & Trivelpiece, S. G. The winter distribution of chinstrap penguins from two breeding sites in the South Shetland Islands of Antarctica. *Polar Biol* **30**, 1231-1237, doi:10.1007/s00300-007-0283-1 (2007).
74 Polito, M. J. *et al.* Stable isotope analyses of feather amino acids identify penguin migration strategies at ocean basin scales. *Biol Letters* **13**, doi:10.1098/rsbl.2017.0241 (2017).
75 Iwata, T. *et al.* Using a mandible accelerometer to study fine-scale foraging behavior of free-ranging Antarctic fur seals. *Marine Mammal Sci* **28**, 345 - 357 (2012).
76 Reid, K., Croxall, J. P., Briggs, D. R. & Murphy, E. J. Antarctic ecosystem monitoring: quantifying the response of ecosystem indicators to variability in Antarctic krill. *Ices J Mar Sci* **62**, 366-373, doi:DOI 10.1016/j.icesjms.2004.11.003 (2005).
77 Reid, K. & Forcada, J. Causes of offspring mortality in the Antarctic fur seal, Arctocephalus gazella: the interaction of density dependence and ecosystem variability. *Can J Zool* **83**, 604-609, doi:10.1139/Z05-045 (2005).
78 Croxall, J. P., Reid, K. & Prince, P. A. Diet, provisioning and productivity responses of marine predators to differences in availability of Antarctic krill. *Marine Ecology-Progress Series* **177**, 115-131 (1999).
79 Lynnes, A. S., Reid, K. & Croxall, J. P. Diet and reproductive success of Adelie and chinstrap penguins: linking response of predators to prey population dynamics. *Polar Biol* **27**, 544-554, doi:DOI 10.1007/s00300-004-0617-1 (2004).
80 Lynnes, A. S., Reid, K., Croxall, J. P. & Trathan, P. N. Conflict or co-existence? Foraging distribution and competition for prey between Adelie and chinstrap penguins. *Marine Biology* **141**, 1165-1174, doi:DOI 10.1007/s00227-002-0899-1 (2002).
81 Bernard, K. S. & Steinberg, D. K. Krill biomass and aggregation structure in relation to tidal cycle in a penguin foraging region off the Western Antarctic Peninsula. *Ices J Mar Sci* **70**, 834-849, doi:DOI 10.1093/icesjms/fst088 (2013).
82 Hinke, J. T., Polito, M. J., Reiss, C. S., Trivelpiece, S. G. & Trivelpiece, W. Z. Flexible reproductive timing can buffer reproductive success of Pygoscelis spp. penguins in the Antarctic Peninsula region. *Mar Ecol Prog Ser* **454**, 91-104, doi:Doi 10.3354/Meps09633 (2012).

83 Trivelpiece, W. Z. *et al.* Variability in krill biomass links harvesting and climate warming to penguin population changes in Antarctica. *Proceedings of the National Academy of Sciences*, doi:10.1073/pnas.1016560108 (2011).
84 Miller, A. K., Karnovsky, N. J. & Trivelpiece, W. Z. Flexible foraging strategies of gentoo penguins Pygoscelis papua over 5 years in the South Shetland Islands, Antarctica. *Marine Biology* **156**, 2527-2537, doi:DOI 10.1007/s00227-009-1277-z (2009).
85 Busser, C., Kahles, A. & Quillfeldt, P. Breeding success and chick provisioning in Wilson's storm-petrels Oceanites oceanicus over seven years: frequent failures due to food shortage and entombment. *Polar Biol* **27**, 613-622, doi:10.1007/s00300-004-0627-z (2004).
86 Friesen, V. L., Burg, T. M. & Mccoy, K. D. Mechanisms of population differentiation in seabirds. *Molecular Ecology* **16**, 1765-1785, doi:DOI 10.1111/j.1365-294X.2006.03197.x (2007).
87 Wynen, L. P. *et al.* Postsealing genetic variation and population structure of two species of fur seal (Arctocephalus gazella and A. tropicalis). *Molecular Ecology* **9**, 299-314, doi:doi:10.1046/j.1365-294x.2000.00856.x (2000).
88 Hoffman, J. I., Trathan, P. N. & Amos, W. Genetic tagging reveals extreme site fidelity in territorial male Antarctic fur seals Arctocephalus gazella. *Molecular Ecology* **15**, 3841-3847, doi:doi:10.1111/j.1365-294X.2006.03053.x (2006).
89 Ainley, D. G., Nur, N. & Woehler, E. J. Factors affecting the distribution and size of pygoscelid penguin colonies in the Antarctic. *Auk* **112**, 171-182 (1995).
90 Kokubun, N., Takahashi, A., Mori, Y., Watanabe, S. & Shin, H. C. Comparison of diving behavior and foraging habitat use between chinstrap and gentoo penguins breeding in the South Shetland Islands, Antarctica. *Marine Biology* **157**, 811-825, doi:DOI 10.1007/s00227-009-1364-1 (2010).
91 Miller, A. K., Kappes, M. A., Trivelpiece, S. G. & Trivelpiece, W. Z. Foraging-Niche Separation of Breeding Gentoo and Chinstrap Penguins, South Shetland Islands, Antarctica. *The Condor* **112**, 683-695, doi:10.1525/cond.2010.090221 (2010).
92 Takahashi, A. *et al.* Foraging strategies of chinstrap penguins at Signy Island, Antarctica: importance of benthic feeding on Antarctic krill. *Marine Ecology-Progress Series* **250**, 279-289 (2003).
93 Barlow, K. E. *et al.* Are penguins and seals in competition for Antarctic krill at South Georgia? *Marine Biology* **140**, 205-213, doi:DOI 10.1007/s00227-001-0691-7 (2002).
94 Barlow, K. E. & Croxall, J. P. Seasonal and interannual variation in foraging range and habitat of macaroni penguins Eudyptes chrysolophus at South Georgia. *Marine Ecology-Progress Series* **232**, 291-304 (2002).
95 Barlow, K. E. & Croxall, J. P. Provisioning behaviour of Macaroni Penguins Eudyptes chrysolophus. *Ibis* **144**, 248-258 (2002).
96 Cresswell, K. A., Wiedenmann, J. & Mangel, M. Can macaroni penguins keep up with climate- and fishing-induced changes in krill? *Polar Biol* **31**, 641-649, doi:10.1007/s00300-007-0401-0 (2008).

600