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BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

► CHAPTER 5.30. CHEMOSYNTHETIC COMMUNITIES

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THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

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5.30. Chemosynthetic Communities

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1. Introduction

In 1977, in the Galápagos Rift, remarkable oases characterised by dense thickets of giant tube worms, large clams and mussels were discovered around deep-sea hydrothermal vents (Corliss *et al.* 1979). These are areas mainly along mid-ocean ridges where hot, chemically enriched fluids spewed from the seabed. It was soon realised that abundant microbial life around the Galápagos vents fixed carbon in-situ by chemolithotrophy using hydrogen sulphide (H₂S) as an energy source and that these bacteria were grazed on by vent animals such as limpets (Jannasch & Wirsén 1979). Subsequently investigations of the anatomy, carbon isotopes, and biochemistry of the giant tubeworm, *Riftia pachyptila* (Cavanaugh *et al.* 1981, Felbeck 1981, Jones 1981, Rau 1981) identified that the worms derived their nutrition from sulphur bacteria harboured in their tissues, a new phenomenon known as chemoautotrophic symbiosis (Dubilier *et al.* 2008). It was soon realised that as well as H₂S, methane (CH₄) and other chemical species that occurred in hydrothermal fluids were also used as energy sources by chemoautolithotrophic bacteria (Jannasch & Mottl 1985). The discovery of life in extreme conditions around hydrothermal vents has changed human perception of the limits to life on Earth and our understanding of the potential for life elsewhere in the solar system and beyond. Vents are also recognised as a possible place for the origin of life on Earth and sources of novel biomolecules for biotechnological applications.

Hydrothermal vents occur along the rifts or flanks of mid-ocean ridges and also at back-arc basins and non-ridge associated seamounts where seawater penetrates the ocean crust and comes into contact with hot basalt beneath, usually associated with a magma chamber. Complex chemical exchanges take place between the basalt and seawater producing a hydrothermal end-member fluid that is enriched in hydrogen sulphide, methane, iron, manganese and other trace metals (Van Dover 2000). Vent fluids also have a lower or higher salinity than seawater, are usually acidic (e.g. East Scotia Ridge vents; Rogers *et al.* 2012), although they can be highly alkaline (e.g. Lost City vent field, Mid Atlantic Ridge, Kelley *et al.* 2001), and have low or zero oxygen content (Van Dover 2000). The fluid becomes buoyant and rises to the surface of the seabed where it can exit as a high temperature black smoker (>300°C), a lower temperature white smoker (100–300°C) or as low temperature diffuse flow (usually <40°C; Van Dover 2000). Since the discovery of vents at the Galápagos Rift they have been detected in all the major world oceans at depths from the intertidal (e.g. Bright *et al.* 2003) to 4960 m depth (Connelly *et al.* 2012), but discoveries of vents at high latitudes have taken place slowly (e.g. Pedersen *et al.* 2010, Rogers *et al.* 2012) because of the difficulties of exploring deep-sea ecosystems at high latitudes (Macpherson *et al.* 2005). The fauna of hydrothermal vents comprises a small set of specialised taxa (>700 species) that are >70% endemic to vents (Wolff 2005). Communities are often visually dominated by a relatively few species, although repeated sampling of the best-studied vent communities reveal that accumulation of species fails to reach asymptote and ~50% of species are represented by a few individuals (Van Dover 2003). The composition of communities varies from ocean to ocean reflecting differences in geology, especially important in determining the spatial distribution and longevity of vent fields, but also geochemistry and long-term biogeographic influences on the evolution of regional vent faunas (Bachraty *et al.* 2009, Van Dover 2011, Rogers *et al.* 2012). Within a region, geological setting and geochemistry also play a significant role in variation of the structure of vent communities. However, at this scale the local history of vents, which determines their state of succession, and their proximity to other similar communities, becomes important (e.g. Tunnicliffe & Juniper 1990, Shank *et al.* 1998). At the scale of individual vent fields and individual vents the biota typically occupies the interface between vent fluids and cold seawater. Strong physico-chemical gradients drive a zonation of species and life history stages with decreasing tolerance to harsh conditions moving away from fluid emanations until a normal deep-sea fauna is present (Marsh *et al.* 2012).

Following the discovery of chemoautotrophic symbiosis at hydrothermal vents it was discovered in other shallow and deep-water environments where there were high concentrations of sulphide, methane or other reduced inorganic chemicals associated with the presence of high levels of hydrocarbons or other organic material (Dubilier *et al.* 2008, Bernardino *et al.* 2012). These included cold seeps, large food falls, such as whale carcasses, wood and kelp and also a variety of shallow-water and deep sediments of coastal wetlands, estuaries, organically enriched shelves, and also slope habitats in areas of high surface primary productivity (Dubilier *et al.* 2008, Bernardino *et al.* 2012).

Cold seeps occur where reduced sulphur or methane emerge from the seafloor without a large rise in temperature (Levin 2005). They were initially discovered in the Gulf of Mexico where hypersaline fluids enriched in ammonium (NH₄) and H₂S seep from the base of a steep carbonate escarpment and support chemosynthetic communities. These comprised siboglinid tube worms, mussels, vesicomyid clams, limpets, galatheid squat lobsters, zoarcid fish and other species with close phylogenetic relationships to species from hydrothermal vents on the East Pacific Rise (Paull *et al.* 1984, 1985, Levin 2005). Since this discovery cold seeps have been found

all around the world's oceans on active and passive continental margins and at a range of depths from intertidal to >7000 m (Levin 2005). The geological settings of seeps are highly diverse and they originate through a variety of processes and manifest on the seabed in a variety of ways. Seeps can arise through several processes including convergent plate tectonics (particularly subduction), the compaction and overpressuring of sediments by sedimentary overburden, gas hydrate dissociation, subsurface salt migration and mineral dehydration reactions (Levin 2005, Cordes *et al.* 2010). The seeps are based on methane, other hydrocarbon gases or gas hydrates which migrate along pathways of permeability such as rock fractures or faults, layers of sediment or mud diapirs (Levin 2005). H₂S is thought to be produced mainly through microbial anaerobic oxidation of methane (AOM), by bacterial and archaeal consortia (e.g. Boetius *et al.* 2000), that is coupled to sulphate reduction and the production of bicarbonate (Levin 2005). Thus cold seeps are often associated with the formation of carbonate mounds or platforms that can provide hard substrata for non-chemosynthetic sessile organisms such as cold-water corals. Other forms of surface expression of seeps include the escape of bubbles of gas from the seabed, the formation of shallow seabed depressions, known as pockmarks, mud volcanoes, mud diapirs or ridges, the occurrence of brine pools on the seabed, the presence of outcropping gas hydrates, or seeping oil, visible on the sea surface (Van Dover 2000, Levin 2005, Cordes *et al.* 2010).

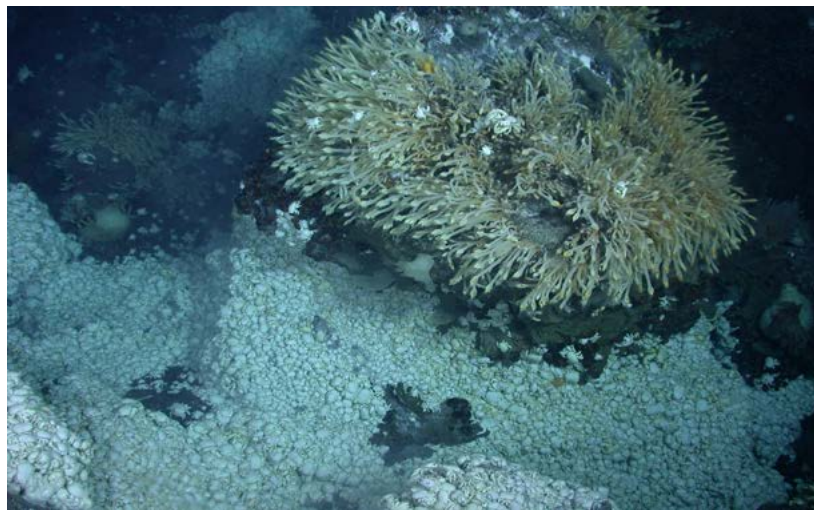
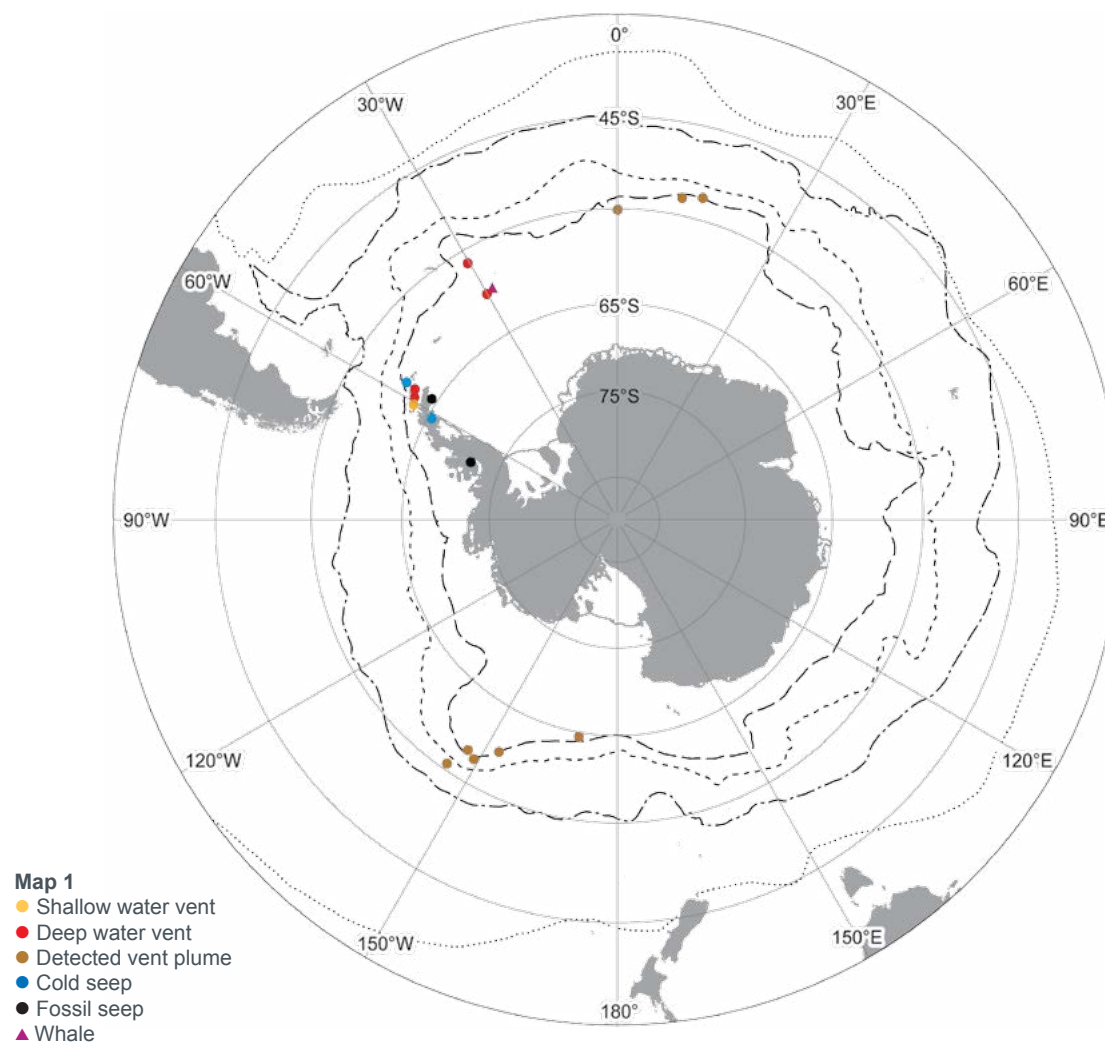


Photo 1 East Scotia Ridge hydrothermal vent community on the E9 segment, 2397 m depth, showing aggregations of the yeti crab *Kiwa* n. sp. and the stalked barnacle *Vulcanolepas scotiaensis*. Photo taken by ROV *Isis* Dive 138, ChEsSo Consortium Project Cruise James Cook JC42, 2010.

The biota of cold seeps in the deep sea varies geographically but these ecosystems tend to be visually dominated by microbial mats and symbiont-hosting megafauna including vesicomyid, solemyid, lucinid and thyasirid clams, bathymodiolid mussels, siboglinid polychaete worms, including vestimentiferan tubeworms, frenulate and monoliferan Pogonophora and cladorhizid sponges (Levin *et al.* 2005, Cordes *et al.* 2010, Bernardino *et al.* 2012). There can also be high densities of sediment infauna at cold seep ecosystems including both meiofauna and macrofauna, although this is not always the case and sometimes abundance of these size classes of organisms can be reduced compared to surrounding communities (Levin 2005, Bernardino *et al.* 2012). Up to around 600 species of seep fauna have been described and levels of endemism can be high (up to ~40%; German *et al.* 2011) but varies markedly from site to site and region to region. There is a suggestion that endemism is highest amongst species with symbionts and tends to increase with increasing depth (Levin 2005, Bernardino *et al.* 2012). Seep sites often also host significant numbers of non-obligate species although these tend to be tolerant to the adverse chemical conditions present at some of these sites (e.g. high levels of sulphide and low levels of oxygen; Levin 2005). In some cases close faunal similarities have been detected amongst seep sites at similar depths but separated by considerable distances (e.g. eastern and western Atlantic equatorial belt; Olu *et al.* 2010). Overall depth appears to have strong influence on the composition of cold seep communities globally (Levin 2005, Olu *et al.* 2010, Bernardino *et al.* 2012). As with hydrothermal vent ecosystems at a local level, zonation of fauna is found around seep ecosystems with the taxa most tolerant to reducing conditions (e.g. high concentrations of sulphide and low concentrations of oxygen) found close to sources of seepage (Levin 2005). The diversity of seep fauna is often partially dependent on the generation of biogenic habitat by species that add structure to the environment (ecosystem engineers; Cordes *et al.* 2010, Bernardino *et al.* 2012).

Following the discovery of cold seeps it was also discovered that the arrival of whale carcasses, large pieces of wood or kelp at the seabed could also generate communities of animals hosting chemoautotrophic symbionts.



Chemosynthetic communities Map 1 Distribution of known chemosynthetic communities and sites where deep-sea hydrothermal vent sites are known to occur.

In such cases the anaerobic decomposition of organic material coupled with sulphate reduction also resulted in the generation of H_2S . In the case of large whale carcasses this process occurs after the initial consumption of the soft tissues of the whale by mobile scavengers and the development of a community of heterotrophic organisms deriving nutrition from large quantities of organic material associated with the whale skeleton and surrounding sediments. After several years H_2S generation from the microbial decomposition of lipids in the whale bones initiates the development of a chemosynthetic community. This sulphophilic stage can last for tens of years and can generate high density communities of both sulphide-tolerant heterotrophic organisms as well as those hosting chemoautotrophic bacteria. These can include high densities of polychaetes (e.g. dorvilleids), mussels (e.g. *Idas*), pyropeltid and cocculinid limpets, provannid and columbellid gastropods, vesicomyid and lucinid clams, isopods and siboglinid worms (vestimentiferan tube worms; Smith & Baco 2003). The diversity of sulphophilic whale fall communities is quite high (>400 species; Smith & Baco 2003) and a significant proportion of these species appear to be specialists of whale carcasses. Another specialist group of organisms that have been found on whale bones are the siboglinid polychaetes of the genus *Osedax* (Rouse *et al.* 2004). These worms have a bulbous ovisac with a sheath which is continuous with a system of root-like branches that penetrate the whale bone which the worm inhabits (Rouse *et al.* 2004). The sheath contains bacteria of the order Oceanospirillales known to be able to heterotrophically degrade complex organic molecules (Rouse *et al.* 2004). These bacteria are symbionts of the worms but are heterotrophic rather than chemoautotrophic (Rouse *et al.* 2004).

Other forms of food falls such as wood and kelp also appear to attract high densities of opportunistic organisms characteristic of organically enriched marine ecosystems. However, these different types of food falls differ markedly in their speed of decomposition, their development of sulphide tolerant or dependent communities and the timescales over which they exert an influence on the seabed (Bernardino *et al.* 2010). It is important to note that some species appear to be shared between whale falls and other types of food-fall (e.g. wood and kelp), cold seeps and even hydrothermal vents and there are likely to be evolutionary links between these faunas (Smith & Baco 2003, Bernardino *et al.* 2010, 2012).

2. Southern Ocean chemosynthetic communities

As stated above the discovery of chemosynthetic ecosystems in the Antarctic has taken place slowly compared to at mid- and low-latitudes. This is because of the extreme isolation of Antarctic marine ecosystems meaning that exploration is extremely expensive. It is also because of the extreme conditions in terms of low temperatures, the presence of ice and the frequent occurrence of poor weather and associated sea states. The waters of the Southern Ocean and coastal seas of Antarctica remain largely unexplored for chemosynthetic ecosystems. Even where hydrothermal signatures have been detected subsequent exploration of the seabed and identification and documentation

of associated ecosystems has taken many years or has not taken place to date (Map 1). This represents a significant gap in our understanding of the biogeography and evolution of chemosynthetic ecosystems globally as the Southern Ocean potentially represents an important pathway of connectivity between the other major oceans of the world both through the eastward flow of the Antarctic Circumpolar Current (e.g. Van Dover *et al.* 2002) and the connections between Antarctica and the global deep sea through the thermohaline circulation (e.g. Strugnell *et al.* 2008). This gap in knowledge has only been partially addressed for hydrothermal vent ecosystems with the recent discovery of high-temperature deep-sea hydrothermal vents in the Scotia Sea along with endemic chemosynthetic communities (Rogers *et al.* 2012) but exploration of other forms of chemosynthetic communities are few. In 2008 SCAR started SAVAnt, the seeps and vents in Antarctica Action Group, to identify areas likely to contain hydrothermal vents and cold seeps based on gravity, bathymetry, geophysical and oceanographic data.

2.1. Chemosynthetic communities from the past

To date, two fossil Antarctic seep sites are known: a single small Late Jurassic seep deposit from Alexander Island (Kelly *et al.* 1995), and a group of seeps in the Late Cretaceous (Maastrichtian) on Snow Hill Island in the James Ross Basin (Map 1). The Late Jurassic deposits include aggregations of a small gastropod, *Hokkaidoconcha hignalli* as well as a limpet, lucinacean and small protobranch bivalves (Kelly *et al.* 1995, Kaim & Kelly 2009). Overall the fossilised community appears to resemble fossil Cretaceous hydrocarbon seeps from Japan (Kaim & Kelly 2009). The Cretaceous seeps are some of the best exposed and largest ancient examples in the world and have never been properly investigated (Campbell 2006). The Late Cretaceous cold seep deposits are located on the Spath Peninsula at the northern tip of Snow Hill Island. They occur in the 170 m thick Karlsen Cliffs Member, which is a component of the extensive Snow Hill Island Formation (Pirrie *et al.* 1997). Seep deposits also occur on the south western tip of Seymour Island in the same formation. The predominant lithologies within the Snow Hill Island Formation comprise mudstones, silty mudstones and heavily bioturbated sandstones, and the associated faunal assemblages are indicative of mid- to outer-shelf depths. A combination of palaeontological and Sr isotope age controls are strongly indicative of a basal Maastrichtian age (~71 Ma) for the cold seep deposits in the Karlsen Cliffs Member (Crame *et al.* 2004). The seeps are exposed as large columns of rock, up to 10 m tall and ~5 m wide, sitting within fine-grained, unconsolidated marine silts and sands. At least 12 are present in the sequence. The columns are composed of carbonate cemented sediment with a high abundance but low diversity fauna consisting primarily of the thyasirid bivalve *Thyasira townsendi*. These bivalves also occur in thin, discrete layers in the overlying Snow Hill Island and Lopez de Bertodano formations, but not with associated carbonate deposits (Pirrie *et al.* 1997) and became extinct after the K-T boundary.

2.2. The biogeography and depth distribution of chemosynthetic communities in the present day

2.2.1. Hydrothermal vent communities

It is fascinating to note that in 1971 photographs were published from 2377 m depth on the southern part of the East Scotia Ridge showing communities of barnacles and other fauna (Newman & Ross 1971) that we now recognise as vent-endemic (Rogers *et al.* 2012). This predated the discovery of deep-sea hydrothermal vents at the Galápagos Rift and at the time these were not recognised as anything unusual perhaps because of the high abundance of benthic fauna seen elsewhere around the Antarctic. More than twenty years later shallow-water and deep-water hydrothermal vents were identified in and around the South Shetland Islands lying off the Antarctic Peninsula (Rey *et al.* 1995, Klinkhammer *et al.* 1996, 2001, Bohrmann *et al.* 1999, Dähmann *et al.* 2001, Petersen *et al.* 2004, Somoza *et al.* 2004; Map 1). Shallow water hydrothermal vents are present at Deception Island, a flooded caldera with a single opening to the sea known as Neptune's Bellows (Rey *et al.* 1995). Inside the caldera which is down to 160–180 m in depth, a number of structures have been observed including sharp relief volcanic cones, up to 50 m in height, low and high relief mounds, spire like structure and acoustically transparent zones where the structure of the volcanic sediments are disrupted by a gaseous fluid flow (Rey *et al.* 1995, Somoza *et al.* 2004). In some cases these structures are surrounded by a halo of high concentrations of elements likely to be associated with hydrothermal emissions (e.g. Mn and Zn; Somoza *et al.* 2004). Overall evidence suggests that the seafloor of the flooded caldera of Deception Island contains sediment-hosted hydrothermal vents which although they have been imaged acoustically have not actually been filmed or photographed to date. Whether or not these structures host vent-endemic communities is unknown. Investigation of the sediments associated with intertidal/shallow subtidal fumeroles in Fumerole Bay, Deception Island has identified a moncelid platyhelminth which is covered in a dense layer of bacteria living in a mucus coat (Bright *et al.* 2003). This animal is tolerant of elevated temperatures (50% survival at 30°C for 48 hrs; Bright *et al.* 2003). It becomes more dominant in the meiofaunal community in the vicinity of fumerole areas and relatively less common (and other meiofauna more common) moving at increasing distances away from warm sediments. Overall meiofaunal densities were an order of magnitude lower in warm sediment areas and other members of the community included copepods, nematodes, other flat worms and low numbers of oligochaetes, polychaetes, ostracods and mites (Bright *et al.* 2003). Shallow-water hydrothermal vents have also been reported from depths of ~200 m off Franklin Island in the Western Ross Sea (McGillivray *et al.* 2005). As yet these do not appear to have been investigated for evidence of chemosynthetic communities.

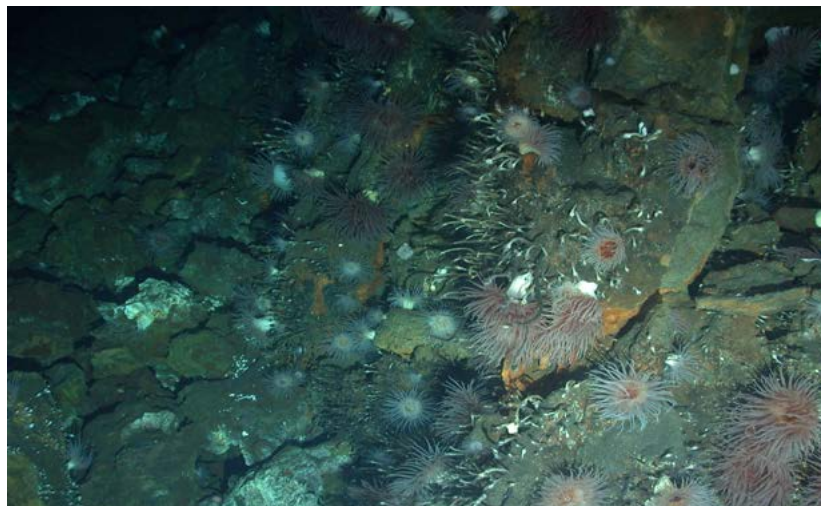


Photo 2 East Scotia Ridge hydrothermal vent community on the E9 segment, 2400 m depth, located around diffuse fluid flow including actinostolid anemones and *Vulcanolepas scotiaensis*. Photo taken by ROV *Isis* Dive 140, ChEsSo Consortium Project Cruise James Cook JC42, 2010.

Hydrothermal vents have been identified between the South Shetland Islands and the Antarctic Peninsula in the Bransfield Strait, a marginal basin area with a region of central rifting running from the north east to the south west spreading at about 1 cm per year (Petersen *et al.* 2004; Map 1). The basin is sediment covered to a depth of up to approximately 3.3 km and several neovolcanic centres occur along the inferred rift axis, parallel to the South Shetland Islands and lying between Deception Island in the south and Clarence Island to the north (Petersen *et al.* 2004). Hydrothermal venting has been detected at these centres through the detection of hydrothermal plumes, sampling of hot sediments (42–48.5°C) and the identification of hydrothermal precipitates on the seabed and are located on the Hook Ridge and the Three Sisters Ridge (Bohrmann *et al.* 1999, Dähmann *et al.* 2001, Klinkhammer *et al.* 2001). Phase separation of hydrothermal end-member fluids probably takes place below the seabed within the crust underneath the Hook Ridge (Dähmann *et al.* 2001) although the fluids are diluted on their way to the seabed and altered through contact with organically rich sediment. Polymetallic sulphides occur on the Hook Ridge along with crusts of barite, marcasite and pyrite and protuberances of iron oxyhydroxide (Petersen *et al.* 2004). The mineralogy of the sulphides on these ridges indicate a high sulphidation state and a chemistry similar to some back-arc vent sites (Petersen *et al.* 2004).

The only fauna observed on the surface at these vents were high densities of ophiuroids. However, sampling of the vent sediments revealed siboglinid worms from the genus *Siboglinum*. This species is thought to host sulphur symbionts because the low concentrations of methane in the Hook Ridge sediments (<25 $\mu\text{mol L}^{-1}$) are unlikely to allow symbiosis with methanotrophic bacteria (Sahling *et al.* 2005). However, the explanation for a lack of other vent-endemic fauna at these hydrothermal vents is thought to be related to the low concentrations of H_2S in near-surface sediments. Although the H_2S concentration of the vent end-member fluid is thought to be >4.5 mmol L^{-1} the concentrations in the warm sediment at the posterior end of the worms is only ~150 $\mu\text{mol L}^{-1}$ as a result of dilution by seawater and removal as metal sulphide precipitates (Sahling *et al.* 2005). Sulphur isotope studies indicate that a significant proportion of the sulphide associated with hydrothermal precipitates in the Hook Ridge system are derived from anaerobic oxidation of organic material in the sediments of the basin coupled to seawater sulphate reduction (Petersen *et al.* 2004).

To date the most spectacular deep-sea hydrothermal vent endemic communities in the Antarctic have been found along the East Scotia Ridge (ESR), located in the Scotia Sea in the Atlantic sector of the Southern Ocean (Map 1, Photos 1–2). Spreading at the East Scotia Ridge began about 15 million years ago (Larter *et al.* 2003) and the current rate is at ~70 mm yr^{-1} .



Photo 3 South Sandwich Islands whale fall community at 1445 m depth comprising *Osedax* and limpets (*Lepetodrilus* sp.; Amon *et al.* 2013). Photo taken by ROV *Isis* Dive 148, ChEsSo Consortium Project Cruise James Cook JC42, 2010.

The ridge is split into nine second-order ridge segments (E1–E9) which are separated by non-transform discontinuities and is about 500 km long (Livermore 2003). E3 to E8 have well-developed rift valleys but E2 and E9 are smooth axial volcanic highs with a magma chamber underlying E2 and probably another underlying E9 (German *et al.* 2000). Hydrothermal plumes were detected in the water column over the ridge segments E2 and E9 using a light scattering sensor and for E9 also through the detection of anomalously high manganese concentrations (German *et al.* 2000). In 2009 these vents were located through a combination of CTD (conductivity, temperature, depth) casts to identify the hydrothermal plumes and also towed camera survey. This was followed in 2011 by survey and sampling with the remotely operated vehicle (ROV) *Isis*. The E2 vent field is located mainly along a fissure which intersects with a fault associated with the axial volcanic high at a depth of ~2600 m. It is associated with numerous chimneys up to 15 m high venting clear fluid at up to 352.6°C which form black smokers as metallic sulphides in the fluid precipitate on mixing with seawater at ambient temperature (~0.0°C). Diffuse venting also occurs on this field at temperatures of 3.5–19.9°C. At the E9 site the vents are located in fissures lying across relatively flat sheet lavas just north of a major collapse feature on the ridge (Devil's Punchbowl) at a depth of approximately 2400 m. The vents in this area produce fluids at different temperatures with the hottest reaching 382.8°C and cooler vents at up to 351°C but overall with lower chlorinities and higher levels of H_2S (9.5–13.6 mM) than at E2 (7.0 mM; Rogers *et al.* 2012).

The fauna at the ESR vents is broadly similar but with a higher abundance and biomass and also species diversity at E9 versus E2, possibly reflecting higher concentrations of H_2S and microbial primary production (Rogers *et al.* 2012). The vents are visually dominated by high densities (>4000 individuals m^{-2} in some aggregations) of a new species of yeti crab (*Kiwa* n. sp.), a large peltospiroid gastropod, stalked barnacles (*Vulcanolepas scotiaensis*) and large actinostolid sea anemones (Rogers *et al.* 2012, Marsh *et al.* 2012, Buckeridge *et al.* 2013). The first three of these species potentially host either epibiotic sulphur bacteria (*Kiwa* n. sp. and possibly *Vulcanolepas scotiaensis*) or endosymbiotic sulphur bacteria (peltospiroid gastropod), whilst the anemones are predators (Reid *et al.* 2013). There are also limpets (*Lepetodrilus* n. sp.) which are found grazing on many of the surfaces within the vent fields, including on other animals, as well as several other species of gastropods (see Table 1 & Rogers *et al.* 2012). Other predators include a stichasterid seastar, observed feeding on yeti crabs and barnacles, carnivorous sponges (*Cladorhiza* sp.), pycnogonids (*Sericosura* spp. as well as non-vent Antarctic species on the vent periphery such as *Colossendeis* sp.), an unidentified octopus and zoarcid fish (Rogers *et al.* 2012, Reid *et al.* 2013). Most of these animals are undescribed at the species or higher taxonomic levels. In addition, it is notable that other groups typically found on hydrothermal vents, including siboglinid worms, alvinocarid shrimps, bathymodiolid mussels and

bythograeid crabs were absent from these vents (Rogers *et al.* 2012). Overall the ESR vents appear to represent a new biogeographic province when species comparisons are undertaken globally using multivariate analysis (Rogers *et al.* 2012). That the majority of species found associated with the ESR vents are novel and the community structure associated with these vents is, to date, unique, especially in terms of the high abundance of yeti crabs and the occurrence of predators such as the seastar also emphasises the regional character of this biota (Rogers *et al.* 2012).

Table 1 Dominant fauna at East Scotia Ridge vents E2 and E9 (Rogers *et al.* 2012).

	E2	E9
Porifera		
Cladorhiza	Cladorhiza n. sp. 1	Cladorhiza n. sp. 1 Abyssocladia n. sp. 1
Cnidaria Anthozoa		
Hormathiidae		Chondrophellia sp. or Hormathia spinosa
Actinostolidae	Actinostolidae n. sp. 2 Actinostolidae n. sp. 2 Actinostolidae n. sp. 3 Actinostolidae n. sp. 3 Actinostolidae n. sp. 4	Actinostolidae n. sp. 1 Actinostolidae n. sp. 2 Actinostolidae n. sp. 3
Annelida		
Polychaeta	Polynoidae sp. 1	Polynoidae spp. 2, 3 and 4
Mollusca		
Gastropoda	Peltoispiroidea n. sp. cf Protolira sp. Lepetodrilus n. sp.1 Provannid sp. 1	Peltoispiroidea n. sp. cf Protolira sp. Lepetodrilus n. sp.1 Provannid sp. 1 Provannid sp. 2
Cephalopoda		Cephalopoda
Arthropoda		
Cirripedia	Vulcanolepas scotiaensis	Vulcanolepas scotiaensis
Anomura	Kiwa n. sp.	Kiwa n. sp.
Pycnogonida	Sericosura sp. 1 Sericosura sp. 2 Colossendeis cf concedis (vent periphery) Colossendeis cf elephantis (vent periphery)	Sericosura sp. 1 Sericosura sp. 2 Sericosura sp. 3 Colossendeis cf concedis (vent periphery) Colossendeis cf elephantis (vent periphery)
Echinodermata		
Asteroidea		
Stichasteridae	Stichasteridae n. sp.	Stichasteridae n. sp.
Freyellidae	Freyella cf fragilissima	Freyella cf fragilissima
Chordata		
Vertebrata		Zoarcid fish

The fauna of the ESR vents shows a distinct zonation around the vents with the yeti crabs located closest to the source of hydrothermal fluids, peltospirid gastropods located outside this zone and then the stalked barnacles, followed by the actinostolid sea anemones (Marsh *et al.* 2012). Around the vent periphery is a zone occupied by the stichasterid sea stars and other organisms including large sea spiders (*Colossendeis* sp.). A zonation is also seen within the yeti crabs with assemblages of successively smaller animals occurring at successive distances away from high-flow hydrothermal vents (Marsh *et al.* 2012). Changes in assemblage moving away from the vents are also reflected by changes in isotopic composition of tissues of component species indicating changes in nutrition (Marsh *et al.* 2012).

Plumes from deep-sea hydrothermal vents have been detected elsewhere in the Pacific, Atlantic and Indian Ocean sectors of the Southern Ocean. Hydrothermal plume signals in the form of ³He signals have been detected in six areas along the Pacific-Antarctic Ridge including ridge segments between 170°W and 168°W, 151°W and 153°W, small segments at 148°W and 146.5°W and locations at 162°W and 145°W (Winckler *et al.* 2010, Downes *et al.* 2012). Because of the extreme distances involved in exploring the southern portion of the Pacific-Antarctic Ridge the location of these vents have not yet been further constrained.

In the Indian Ocean hydrothermal plumes and hydrothermal mineral deposits have been detected between the Joseph Mayes seamount and Narrowgate segment along the ultraslow spreading South West Indian Ridge (SWIR) between 53°S, 11°E and 52°S, 15°E at depths ~4000 m (Bach *et al.* 2002). The deposits are mainly associated with ultramafic rocks and occur on the northern and southern walls of the rift valley along this segment of the SWIR (Bach *et al.* 2002). Although the position of these vents were well constrained using MAPR (Miniature Autonomous Plume Recorders) arrays these vents also have not been located and investigated for biological communities.

At the end of the SWIR, near the junction with the Mid-Atlantic Ridge, a hydrothermal plume has been detected through iron and manganese anomalies along the 0° meridian (Klunder *et al.* 2011, Middag *et al.* 2011). The plume originates from the Bouvet Triple junction and appears to coincide with the flanks of the Spiess Ridge / Spiess seamount crater (see Ligi *et al.* 1999 for geophysical map of the seamount bathymetry). The origin of this plume has also not been located and so to date observations of the source hydrothermal vents have not taken place.

2.2.2. Cold seeps

Cold seeps were reported from an area previously covered by the Larsen B ice shelf, in the Weddell Sea east of the Antarctic Peninsula. A large area of the seabed (>5500 m²) was reported to be 50–70% covered by bacterial mats with small mounds surrounded by aggregations of clams thought to be *Calyptogena* sp. (Domack *et al.* 2005, Niemann *et al.* 2009). Gas bubbles were also reported to be observed bubbling up from the seabed in places (Domack *et al.* 2005). Return visits to the sites indicated that methane seepage had decreased in the area and that no bubbling gas was observed, bacterial mats were no longer present and no live clams were found (Niemann *et al.* 2008, 2009). Analyses of meiofaunal communities revealed high densities of a single species of nematode from the genus *Halomonhystera* (Hauquier *et al.* 2011). Analyses of stable isotope ratios (¹³C) in the nematode indicated it derived its nutrition from surface primary production not from chemosymbiosis (Hauquier *et al.* 2011). Thus, the high densities of this species were considered to be part of a response to the uncovering of this region of the shelf by the collapse of the Larsen B Ice shelf (Hauquier *et al.* 2011). The fauna of this region was also found to be impoverished for macrofauna and megafauna and overall communities of these size-classes of animals were also responding to the recent collapse of the ice shelf and establishment of a greater supply of surface derived organic material (Gutt *et al.* 2011). Very low methane fluxes were detected in the area and sulphide levels were probably too low at the sediment surface to support megafaunal chemosynthetic communities (Niemann *et al.* 2009). Anaerobic methanotrophic and sulphate reducing archaea and bacteria were present deeper in the sediment (Niemann *et al.* 2009).

There are other reports of seabed structures associated with cold seeps in Antarctica. For example, mud volcanoes have been reported at depths of 1600 m to >2500 m along the South Shetland Shelf off the Antarctic Peninsula (Tinivella *et al.* 2007). Analysis of gas within sediments indicates a mixture of methane, pentane and other hydrocarbons suggestive of a thermogenic source of these gases and the presence of gas hydrates is also suspected (Tinivella *et al.* 2007).

2.2.3. Whale falls

Other type of chemosynthetic communities present in Antarctica are whale falls (Photo 3), especially as Antarctic waters are favoured feeding grounds for baleen whales. In order to test if the larvae of the fauna associated with whale falls north of the Polar Front are present in the Southern Ocean, several whale-bone and wood containing landers were deployed during expeditions in 2008–2010 to the Bransfield Strait and Antarctic Peninsula region (e.g. ACES project Cruise JR179; https://www.bodc.ac.uk/data/information_and_inventories/cruise_inventory/report/jr179.pdf). On recovery of some landers during a later LARISSA cruise, *Osedax* and other species of animals were recovered from the whale bones, but these animals and other elements of the communities associated with them have not yet been described (Smith, pers. comm.) A natural whale fall in an advanced stage of decomposition was discovered in a caldera near the Kemp Seamount and hosted an abundant assemblage of at least nine new macrofaunal species including representatives of *Osedax* sp. and *Lepetodrilus* sp. (Amon *et al.* 2013).

2.3. Biogeographic Processes

As yet it is probably too early in the process of discovery and description of Antarctic chemosynthetic communities to come to any firm conclusions regarding their biogeographic affinities or levels of connectivity at local, regional and oceanic scales. There is some evidence that there are historical connections between the hydrothermal-vent endemic fauna of the ESR and that of the Atlantic (e.g. close relationship of *Lepetodrilus* nov. sp from the ESR and *L. atlanticus* from the Atlantic) and southern Pacific Oceans (e.g. presence of *Kiwa* n. sp. at ESR and *Kiwa hirsuta* on the Pacific-Antarctic Ridge; close relationship of *Vulcanolepas scotiaensis* from the ESR and *V. osheai* from the South West Pacific; Rogers *et al.* 2012). Connectivity may be promoted through stepping-stone-like dispersal between hydrothermal vents located on closely

connected ridge systems running from the Atlantic sector of the Southern Ocean (ESR, American-Antarctic Ridge, Atlantic Indian Ridge), through the Indian Ocean (South West Indian Ridge, South East Indian Ridge) and finally to the Pacific (Pacific-Antarctic Ridge). These ridges comprise many large transform faults that potentially inhibit dispersal (Creasey & Rogers 1999, Vrijenhoek 2010) and the density and depth distribution of vents along them remains unknown. Furthermore, these ridges also cross significant distances of latitude and are thus influenced by both cold and warm water masses, also potentially inhibiting the dispersal of species from one region to another. It is suspected that the lack of many “typical” vent taxa from the ESR



may be a result of the extremely cold waters of the Southern Ocean being unfavourable to species with certain types of life history (e.g. planktotropic larvae) or with physiological limitations preventing life at the low temperatures encountered outside Antarctic vent ecosystems (Rogers *et al.* 2012). The eastward-flowing Antarctic Circumpolar Current may be important in dispersal of vent fauna in the Southern Hemisphere over historical timescales (e.g. Van Dover *et al.* 2002). It is also difficult to reconstruct the history of the present Southern Hemisphere vent fauna given the reconfiguration of ridge systems over millennia. Only further exploration of Southern Ocean and Southern Hemisphere hydrothermal vent and other chemosynthetic ecosystems will reveal the geological, oceanographic and biological factors that have been important in driving the biogeography and evolution of these communities over the large spatial and temporal scales involved.

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THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

Scope

Biogeographic information is of fundamental importance for discovering marine biodiversity hotspots, detecting and understanding impacts of environmental changes, predicting future distributions, monitoring biodiversity, or supporting conservation and sustainable management strategies.

The recent extensive exploration and assessment of biodiversity by the Census of Antarctic Marine Life (CAML), and the intense compilation and validation efforts of Southern Ocean biogeographic data by the SCAR Marine Biodiversity Information Network (SCAR-MarBIN / OBIS) provided a unique opportunity to assess and synthesise the current knowledge on Southern Ocean biogeography.

The scope of the Biogeographic Atlas of the Southern Ocean is to present a concise synopsis of the present state of knowledge of the distributional patterns of the major benthic and pelagic taxa and of the key communities, in the light of biotic and abiotic factors operating within an evolutionary framework. Each chapter has been written by the most pertinent experts in their field, relying on vastly improved occurrence datasets from recent decades, as well as on new insights provided by molecular and phylogeographic approaches, and new methods of analysis, visualisation, modelling and prediction of biogeographic distributions.

A dynamic online version of the Biogeographic Atlas will be hosted on www.biodiversity.aq.

The Census of Antarctic Marine Life (CAML)

CAML (www.caml.aq) was a 5-year project that aimed at assessing the nature, distribution and abundance of all living organisms of the Southern Ocean. In this time of environmental change, CAML provided a comprehensive baseline information on the Antarctic marine biodiversity as a sound benchmark against which future change can reliably be assessed. CAML was initiated in 2005 as the regional Antarctic project of the worldwide programme Census of Marine Life (2000-2010) and was the most important biology project of the International Polar Year 2007-2009.

The SCAR Marine Biodiversity Information Network (SCAR-MarBIN)

In close connection with CAML, SCAR-MarBIN (www.scarmarbin.be, integrated into www.biodiversity.aq) compiled and managed the historic, current and new information (i.a. generated by CAML) on Antarctic marine biodiversity by establishing and supporting a distributed system of interoperable databases, forming the Antarctic regional node of the Ocean Biogeographic Information System (OBIS, www.iobis.org), under the aegis of SCAR (Scientific Committee on Antarctic Research, www.scar.org). SCAR-MarBIN established a comprehensive register of Antarctic marine species and, with biodiversity.aq provided free access to more than 2.9 million Antarctic georeferenced biodiversity data, which allowed more than 60 million downloads.

The Editorial Team



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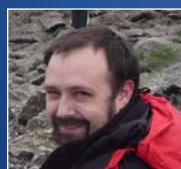
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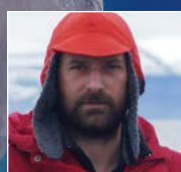
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Yan ROPERT COUDERT spent 10 years at the Japanese National Institute of Polar Research, where he graduated as a Doctor in Polar Sciences in 2001. Since 2007, he is a permanent researcher at the CNRS in France and the director of a polar research programme (since 2011) that examines the ecological response of Adélie penguins to environmental changes. He is also the secretary of the Expert Group on Birds and Marine Mammals and of the Life Science Group of the Scientific Committee on Antarctic Research.

