Chapter 3
Southern Ocean Evolution in a Global Context: A Molecular Viewpoint

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Molecular data can be used to pinpoint both contemporary and historical forces acting on biota but until recently such data have been largely obtained only from vertebrates, such as penguins (Baker et al. 2006), fish (Kuhn and Gaffney 2006; Rogers et al. 2006), and seals (Curtis et al. 2009), whose mobile adult stages are less affected by the barriers imposed by abiotic forces than are invertebrates. Exceptions include research focused on commercially important pelagic taxa, primarily krill (Goodall-Copestake et al. 2010; Batta-Lona et al. 2011). The few early studies on benthic invertebrates indicated the potential use of molecular data in interpretation of Antarctic speciation and connectivity by providing evidence of limited gene flow (Allcock et al. 1997), endemic radiation (Held 2000), cryptic speciation (Held 2003) and historical connectivity between the Antarctic and other oceans (Lörz and Held 2004). Progress was intermittent for several years but a recent surge of molecular data has allowed concepts generally associated with Antarctic biology, but often unproven, to be investigated using genetic methods. Such concepts include the Southern Ocean biota being commonly described as highly endemic (e.g. Brandt et al. 2007a), but in some cases common with the Arctic (Stepanjants 2006); and the biota showing a prevalence of eurybathy (Brey et al. 1996), possessing circumpolar distributions (Clarke and Johnston 2003), and non-dispersive life histories (Pearse et al. 2009). Molecular studies are allowing the strength of these concepts to be tested across a range of taxa with diverse life

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history strategies. Patterns of congruence and conflict are emerging and together these studies are providing a richer understanding of speciation and connectivity within the Southern Ocean ecosystem.

3.1 A Brief Climatic, Oceanographic and Tectonic History of the Southern Ocean

The origins of the Southern Ocean fauna and flora are complex: an endemic biota which has evolved in situ is enriched by organisms that have migrated or dispersed into the Southern Ocean from South America via the Scotia Arc and/or from adjacent deep-water basins (Clarke 2008; Clarke and Crame 2010). Marked shifts in the climatic, oceanographic and tectonic histories of the Antarctic region throughout the Cenozoic (65 Ma-present) must necessarily have played major roles in shaping the extant biodiversity. These shifts are likely to have directly influenced the evolution of the Southern Ocean biota by impacting levels of isolation from, or connectivity to, the world's other ocean basins.

In the early Cenozoic the climate in the Antarctic region was relatively warm and ice free. A deep seaway between the South Tasman Rise and East Antarctica developed about 32 Ma while the Drake Passage probably opened to deep-water flow prior to 29 Ma (Lawver and Gahagan 2003) but possibly not until 24 Ma (Pfuhl and McCave 2007) (Fig. 3.1). Development of the Antarctic Circumpolar Current followed and at around the same time the first continent-wide ice sheet formed. Since the opening of these gateways, the most extensive tectonic activity in the Antarctic has been associated with the formation of the Scotia Sea.

The islands of the Scotia Arc comprise relatively ancient rocks as well as volcanically young rocks (e.g. South Sandwich Islands ∼5 Ma). The floor of the Scotia Sea is relatively young and results from sea-floor spreading over the last 30 million years (Thomson 2004). South Georgia reached its present position by eastward and then northward movement from a position between the Antarctic Peninsula and South America (Lawver and Gahagan 2003).

Almost continual cooling followed the opening of the Tasman Gateway and Drake Passage but a marked decline is detected in the mid-Miocene (c. 14 Ma). This appears to be associated with the formation of the East Antarctic Ice Sheet and is concurrent with increased Antarctic Bottom Water formation and intensification of the global thermohaline circulation (Diekman et al. 2004).

Antarctic ice-sheet size has fluctuated with Milankovitch cycles: ice-core data (EPICA 2004) provide detailed temperature records for the last 800,000 years showing the 100,000 year periodicity of glaciation cycles during this time. Sediment-core data suggest at least 38 cycles, of varying periodicity, in the past 5 million years (Naish et al. 2009). Evidence suggests that the West Antarctic Ice Sheet has collapsed on multiple occasions to allow a trans-Antarctic seaway
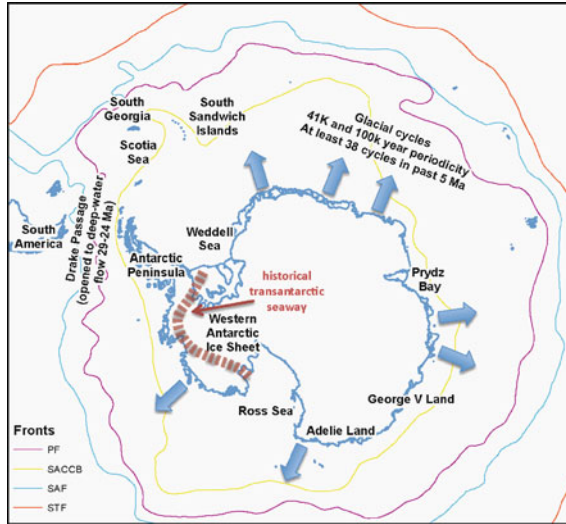
Fig. 3.1 The Antarctic, indicating key locations mentioned in the text, the proposed historical seaway between the Ross Sea and the Weddell Sea (Vaughan et al. 2011), and the important fronts of the Antarctic Circumpolar Current (ACC). The ACC flows clockwise around Antarctica. It is bounded by the Sub Tropical Front (STF) to the north and the Southern Boundary Current (SACCB) to the south, with most of the transport between the sub-Antarctic front (SAF) and the Polar Front (PF). The arrows indicate the movement of ice sheets during glacial cycles

between the Ross and Weddell Seas (Pollard and DeConto 2009). Models suggest this occurred most frequently prior to 3 Ma but has also occurred more recently.

Most evidence for the effects of glacial cycles comes from the last glacial period. Glaciological models, supported by marine geological and geophysical data [see summary in Thatje et al. (2005)] suggest a massive advance of Antarctic ice-sheets during the last glacial maximum (LGM), a fall in global-sea levels and a grounding of ice-sheets out across much of the continental shelf of the Southern Ocean, with a limited number of shelf-edge locations (e.g. western Ross Sea, Prydz Bay, George Vth land) free from grounded ice.

3.2 The Antarctic Circumpolar Current as a Barrier

The Antarctic Circumpolar Current (ACC) marks the boundary between the Southern Ocean and the Atlantic, Pacific and Indian Oceans. Its role in dispersal, and as a barrier to dispersal, has been widely speculated upon. Genetic studies have given more precise information as to how various species interact with the ACC.

A study of the pycnogonid *Colossendeis megalonyx* (Krabbe et al. 2010) showed that the ACC has apparently acted as a vicariant barrier in this species. Six distinct clades or lineages were detected in the study. Five were found only south

of the Polar Front (one unique to Bouvet Island, one occurring at Bouvet Island and the South Sandwich Islands, one at the South Sandwich Islands and Elephant Island, and two additional lineages found only at Elephant Island). The sixth was confined to Burdwood Bank and was sampled from positions north of the sub-Antarctic Front. This non-Southern Ocean lineage appears most closely related to a lineage reported from Bouvet Island, however, the study is based on a short section (561 base pairs) of the barcoding gene and further markers are required to establish the evolutionary relationships of the lineages.

The sea-slug *Doris kerguelensis,* which actually comprises a suite of many cryptic species (Wilson et al. 2009), has also apparently speciated in response to the ACC on several occasions. Wilson et al. (2009) reported three 'trans-Drake' species pairs. In each case, the two species in the pair were sister-taxa in a phylogenetic tree and one lineage was found only in the Bransfield Strait and the other only on the other side of the Drake Passage in South American waters. By applying the best available mutation rate (based on a gastropod molecular clock), the authors suggested that the species within each pair diverged approximately 2 Ma.

Several studies have now estimated the dates of divergence of pairs of species that exist on either side of the ACC. Studies on echinoderms using echinoderm-calibrated molecular clocks indicate that the South American seastar *Odontaster penicillatus* diverged from its Southern Ocean sister species, *O. pearsei,* about 1 Ma (Janosik et al. 2011), the South American sea urchin *Sterechinus agassizi* diverged from its Southern Ocean sister species, *S. neumayeri*, about 5 Ma (Diaz et al. 2011) and that cryptic lineages of the brittle star *Astrotoma agassizi* diverged on either side of the ACC about 1.5 Ma (Hunter and Halanych 2008). González-Wevar et al. (2010) used a relaxed clock method that allows different evolutionary rates on different tree branches to estimate the date at which the Southern Ocean limpet *Nacella concinna* diverged from non-Antarctic *Nacella* species. Using the earliest known dates for various fossils to constrain other nodes on the tree, they estimated divergence to have occurred between about 5 and 9 Ma. Research on limatulids illustrates the very real problems with estimating divergence times (see later). Page and Linse (2000) also used fossil constraints (but with a strict clock) to estimate the date of divergence of the Southern Ocean bivalve *Limatula ovalis* from its sub-Antarctic congener *L. pygmaea*. Considering each of three genes separately, they found widely differing divergence time estimates that ranged from 0.24-2.87 Ma to 6.81 to 19.12 Ma. Nonetheless, these dates are still all after the onset of the ACC, suggesting that the common ancestors of these species were able to cross the ACC, even if the extant species do not.

Evidence that species currently cross the ACC is provided by nemerteans. Thornhill et al. (2008) reported distinct lineages of *Parbolasia corrugata* on either side of the Drake Passage, but a subsequent study by Mahon et al. (2010) detected two lineages that cross the Polar Front in the Drake Passage region.

Similarly, a study of lysianassoid amphipods suggests some lineages do cross the ACC (Havermans et al. 2011). Sampling was concentrated in the Southern Ocean but a single sample of *Orchomenopsis cavimanus* was obtained from the Magellan region (Burdwood Bank). Cryptic speciation was present and one

lineage appeared to be confined to the Scotia Sea. However, the other was found throughout the entire sampling region which extended from the eastern Weddell Sea to the Burdwood Bank in the area of the Sub-Antarctic Front providing some evidence that this species disperses across the ACC close to South America.

Some species may actually use the ACC for dispersal. A molecular study of the notothenioid fish *Gobionothen gibberifrons* noted gene flow was unidirectional and concluded that larval dispersal in the ACC accounted for this (Matschiner et al. 2009).

The sub-Antarctic lineage of the cryptic species complex *Durvillea antarctica*, the buoyant bull kelp, likely disperses in its adult stage throughout the sub-Antarctic islands as algal rafts in the ACC (Fraser et al. 2010). Furthermore, Nikula et al. (2010) found molecular support for a rafting hypothesis in two sub-Antarctic amphipod species commonly found in *D. antarctica* holdfasts. There is also biological evidence in support of rafting in the brooding isopod *Septemserolis septemcarinata*. This species has enlarged pereiopods for climbing onto substrata and only rare dispersal events (the majority from west to east in accordance with flow in the ACC) were required to explain the apparent gene flow between widely spaced populations (Leese et al. 2010) situated within the ACC but on both sides of the Polar Front.

These studies demonstrate that the Polar Front and the ACC do not form an absolute barrier to dispersal and that eddies which spin off north and south are likely to play a role in carrying organisms in and out of the Southern Ocean (Barnes and Clarke 2011). Nonetheless, the wide variation in environmental parameters experienced either side of the Polar Front is likely to hamper the survival of many organisms that cross this potential barrier. In the deep sea, this variation will be less and there is probably a greater likelihood of deep-sea species crossing this barrier. Indeed many truly cosmopolitan species (see later) are found in the deep sea.

3.3 Connectivity with Other Oceans

The exchange of marine species from South American waters with the Southern Ocean has been widely noted (e.g. Dell 1972) and in recent years it has been recognised that fewer Southern Ocean species are endemic than had previously been thought. For example, Griffiths et al. (2009) estimate that the number of Southern Ocean endemics is close to 50 %, meaning that 50 % of species occur either side of this potential barrier. Furthermore they note the increasing presence of endemics with increasing distance from South America, suggesting that the Scotia Arc may be a route of species migration in and out of the Southern Ocean. Certainly this region provides the shortest geographic distance between Southern Ocean and non-Southern Ocean shallow waters, and our knowledge is biased towards shallow waters.

Fig. 3.2 a Phylogenetic relationships of Southern Ocean endemic and deep-sea octopuses. ▶
Bayesian phylogenetic tree based on the results of the relaxed phylogenetic analysis utilizing the
seven genes: *rhodopsin*, *pax-6*, *octopine dehydrogenase* (ODH), 12S rDNA, 16S rDNA,
cytochrome oxidase subunit I (COI) and cytochrome oxidase subunit III (COIII) of 12 Antarctic
octopus species, seven deep-sea octopus species and 15 outgroup taxa. The topology is that from
the posterior sample which has the maximum sum of posterior probabilities on its internal nodes.
Each node in the tree is labelled with its posterior probability, * indicates a posterior probability
of 1.0. The divergence times correspond to the mean posterior estimate of their age in millions of
years. The genera *Adelieledone* (*dark blue*), *Pareledone* (*blue*), and *Megaleledone* (*light blue*) are
endemic to Antarctic waters. The deep-sea genera, *Graneledone* (*red*), *Velodona* (*yellow*), and
Thaumeledone (*orange*) are a monophyletic group and are nested within the Antarctic clade. The
deep-sea clade was estimated to have originated around 33 million years ago (Ma; 95 % HPD
interval 5–64 Ma). The three deep-sea genera were estimated to have diverged from one another
around 15 Ma (95 % HPD interval 1–36 Ma). This figure is an abridged version of that published
in Strugnell et al. (2008). **b** Bayesian phylogenetic tree based on the results of the relaxed
phylogenetic analysis using six genes: *rhodopsin*, 12SrDNA, 16SrDNA, cytochrome oxidase
subunit I (COI), cytochrome oxidase subunit III (COIII) and cytochrome *b* (cyt*b*) of 25
Benthoctopus individuals, 2 *Vulcanoctopus* individuals and 7 outgroup taxa. The topology is that
from the posterior sample which has the maximum product of posterior clade probabilities. Each
node in the tree is labelled with its posterior probability, '*' indicates posterior probability of 1.0.
The divergence times correspond to the mean posterior estimate of their age in millions of years.
The *Benthoctopus* species collected from the Southern Ocean (south of the Polar Front) are
shown in dark blue and represent a paraphyletic group. Other *Benthoctopus* species collected
from the Southern Hemisphere are shown in light blue. *Benthoctopus* and *Vulcanoctopus* species
collected from the Northern Hemisphere are shown in *red*. Outgroup taxa are shown in black. '+'
indicates species that possess an ink sac. Clade1 was estimated to have had a common ancestor
around 16 Ma (95 % HPD interval 4–32 Ma), Clade 2 was estimated to have had a common
ancestor around 5 Ma (95 % HPD interval 1–11 Ma) and Clade 3 was estimated to have had a
common ancestor around 6 Ma (95 % HPD interval 1–13 Ma). Clade 2 was estimated to have
diverged from its sister clade around 14 Ma (95 % HPD interval 4-27 Ma). This figure is an
abridged version of that published in Strugnell et al. (2011)

3.3.1 Southern Ocean: Source and Sink?

Recent phylogenetic studies have demonstrated historical connectivity between the
Southern Ocean and other ocean basins on deep evolutionary timescales. Both
polar emergence and submergence has occurred on Antarctic margins, with taxa
that originated in the deep sea moving into the Southern Ocean and vice versa.

Strong evidence for polar submergence comes from phylogenetic studies of
Asellota isopods (Raupach et al. 2009) based on 18S rRNA sequences, and oc-
topods (Strugnell et al. 2008) employing mitochondrial (12S rRNA, 16S rRNA,
COI, COIII) and nuclear (*rhodopsin, pax-6, ODH*) genes (Fig. 3.2).

Both studies indicate a shallow-water, Southern Ocean origin for clades of these
taxa which invaded the deep sea. Phylogenetic analyses indicate that extant iso-
pods inhabiting the deep sea of the Southern Ocean have arisen multiple times
from shallow water lineages. Divergence-time estimates on the origin and sub-
sequent diversification of the deep-sea octopod clade correspond with the initiation
(~33 Ma) and subsequent intensification (~15 Ma) of the global thermohaline
circulation respectively (Fig. 3.2). These events may have provided oceanographic
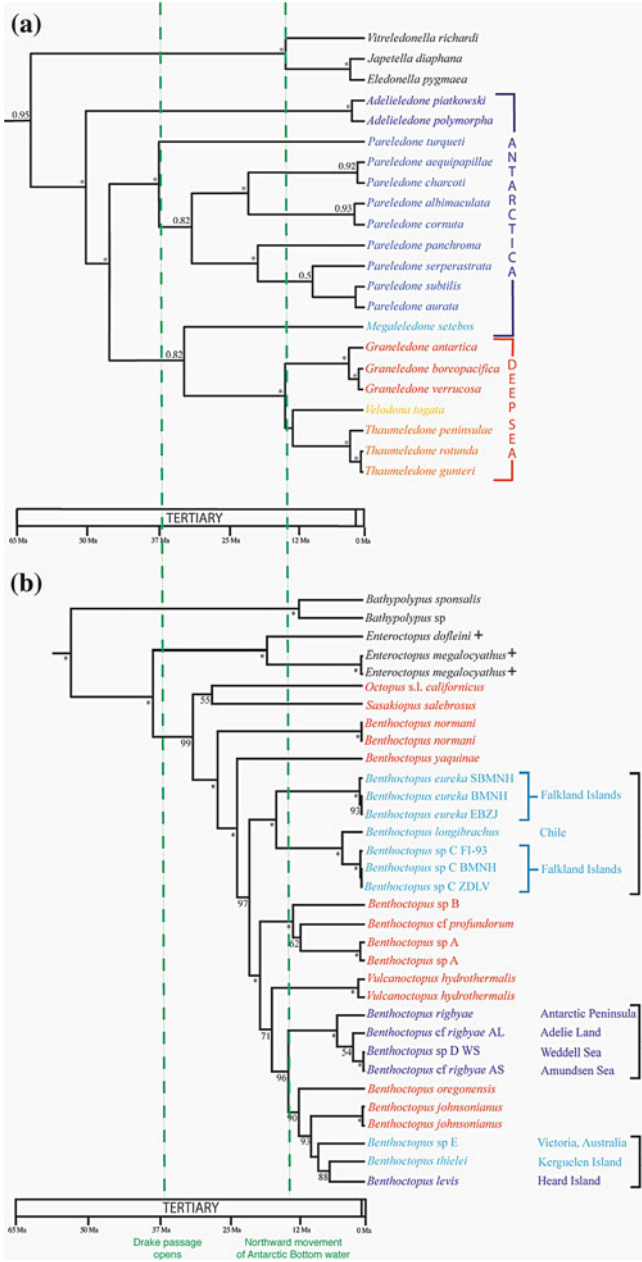
conditions that allowed taxa to move into other deep-sea ocean basins of the world, areas that were previously inhospitable (Strugnell et al. 2008).

Additional climate-driven diversification is apparent in a range of taxa. Speciation and dispersal out of the Southern Ocean in Pleurobranchomorpha (opisthobranch molluscs) have been indicated by a study using two nuclear (18S rRNA, 28S rRNA) and two mitochondrial (16S rRNA, COI) genes (Göbbeler and Klussmann-Kolb 2010). A similar pattern is seen in a study of penguins employing mitochondrial (12S rRNA, 16S rRNA, COI, Cyt*b*) and nuclear (RAG-1) genes (Baker et al. 2006). In both studies, these events were also likely precipitated by the onset of glaciation in Antarctica.

Conversely, evidence for Southern Ocean emergence is seen in the octopod genus *Benthoctopus* which occurs in the deep sea throughout the world's oceans in addition to Southern Ocean waters. Three independent clades within this genus were shown to have colonized the high latitudes in the Southern hemisphere relatively recently (Strugnell et al. 2011) (Fig. 3.2). The timing of the origin of the Southern Ocean *Benthoctopus* clades was estimated to have occurred around 14 Ma. As stated above, intensification of the global thermohaline circulation is understood to have occurred in this time frame providing connections between the deep sea and coastal Antarctic waters. This study therefore suggests that the 'thermohaline expressway' was bidirectional permitting connectivity between the Southern Ocean and the deep sea and also between the deep sea and the Southern Ocean.

Göbbeler and Klussmann-Kolb (2010) also suggest that the opisthobranch *Bathyberthella antarctica* colonized Southern Ocean waters, and estimate this polar emergence to have occurred during a similar timeframe, around 20 Ma.

Although few studies provide dated phylogenies, the increase in global molecular phylogenies is providing evidence of historical connectivity between the Southern Ocean and other ocean basins in a range of taxa, particularly in echinoderms (e.g. O'Loughlin et al. 2011; Mah and Foltz 2011) and crustaceans (e.g. Raupach et al. 2009; Browne et al. 2007).

3.3.2 Difficulties in Dating Evolutionary Events to Relate Them to Climate Change

To constrain or calibrate phylogenetic trees in geological time, it is necessary to use dates obtained from fossils or a known evolutionary rate. Unfortunately many Antarctic fossil beds are covered in ice or have been damaged by the erosion of sediments after glacial maxima. Although some fossil-rich areas exist (e.g. the La Meseta formation, Seymour Island, Antarctic Peninsula), few fossils of Southern Ocean taxa appear suitable for divergence time estimation. For example, the single fossil eleginopid fish on which notothenioid-fish divergence times are based on is controversial (Near 2004; Janko et al. 2007, 2011) and may not even be a notothenioid.

Because molecular evolutionary rates can differ between taxa and lineages, applying an evolutionary rate (estimated from a broader taxonomic group) under the assumption of a 'strict' molecular clock, is only valid where data have been shown to be clock-like. Where suitable fossil calibrations have been available for Southern Ocean taxa, some studies have assumed a strict molecular clock and have been forced to remove non-clock-like data first, for example in Foraminifera (Darling et al. 2004 *partim*) and sea urchins (Lee et al. 2004). In the absence of suitable fossils, other studies have applied evolutionary rates from broader taxonomic groups such as echinoderms (Wilson et al. 2007) and teguline gastropods (Wilson et al. 2009) under the assumption of strict clock. This can give misleading divergence time estimates (e.g. Yoder and Yang 2000). Applying rates from broader taxonomic groups might also be misleading if substitution rates are slower in polar poikilotherms. This has been refuted for 16S rRNA in Antarctic serolid isopods (Held 2001) but has received no further attention.

Other studies have employed relaxed-clock approaches to allow variable rates among lineages without having to remove data. Some of these have fixed fossil dates to particular nodes, for example in Foraminifera (Darling et al. 2004 *partim*), and therefore give apparently precise, but not necessarily accurate, dates without confidence intervals. Others have applied fossil constraints as prior distributions to reflect the uncertainty of the fossil record, for example in octopods (Strugnell et al. 2008). This produces divergence times with broad confidence intervals, making it difficult to link to specific climatic and oceanographic events with certainty.

Future studies should target taxa with multiple, accurately-dated, well-characterized fossils with representatives just above and below the lineages to be dated. The most promising taxa for this are those with hard parts, such as echinoid, gastropod and bivalve families. Alternatively, the application of ancient DNA methodologies to historical museum specimens (collected by early Antarctic explorers) or specimens frozen in situ as was done for Adélie penguins (Lambert et al. 2002) will permit the calculation of relevant evolutionary rates.

3.3.3 Cosmopolitan Species

Connectivity between the Southern Ocean and other ocean basins is found in reports of cosmopolitan and 'bipolar' species (i.e. those found in the Southern Ocean and in Arctic waters). There are many such reports, but few reports are backed up by genetic data. For example, Park and Ferrari (2009) considered the distribution range of all deep-water calanoid copepods found south of the Polar Front. Of these 127 species, 24 were considered endemic to this region, while 84 species had a range that extended beyond the subtropical convergence. Of these 84 species, 29 had ranges thought to extend to sub-Arctic waters whereas another 13 have been reported from the high Arctic. However, increasing numbers of phylogenetic studies in recent years have been highlighting the presence of cryptic

lineages (see later), and molecular data are needed to confirm such widespread distributions.

One of the few studies which provides molecular evidence of truly cosmopolitan species with a range extending from the Arctic Ocean to south of the Antarctic Polar Front was conducted on Foraminifera. Rapidly evolving ITS sequences of three species of benthic foraminiferan species (*Epistominella exigua, Cibicides wuellerstorfi, Oridorsalis umbonatus*) were shown to be almost identical between the Weddell Sea and the Arctic Ocean (Pawlowski et al. 2007). Very similar sequences of the first two species were also obtained from individuals collected from the North Atlantic Ocean, suggesting that each of these species probably exists as massive global populations.

Interestingly, asymmetric gene flow was detected in *E. exigua* with a much stronger signal in the direction from the Southern Ocean to the Arctic, than in the opposite direction (Brandt et al. 2007b). Similar reports of identical SSU rRNA sequences in pelagic foraminifera from the Arctic and the Southern Ocean are also indicative of recent genetic exchange (Darling and Wade 2008).

3.3.4 Bipolar Species

Of the deep-water calanoids thought to occur in both the Arctic and Southern Oceans (Park and Ferrari 2009), six have a reported disjunct distribution. This may be due to lack of sampling, but some authors consider 'bipolar' species to be relatively common. For example Stepanjants (2006) recognised 46 bipolar radiolarian species and 23 bipolar medusozoan species. Although some morphological studies present evidence for bipolar distributions of species, for example in bryozoans (Kuklinski and Barnes 2010), recent claims of 200 + bipolar species (see Kuklinski and Barnes 2010) are likely to be greatly overestimated. Furthermore, detailed taxonomic studies often reveal morphological differences. Bipolarity has been refuted in the sponge species *Stylocordyla borealis* following recent morphological taxonomic work (Uriz et al. 2011) and the Southern Ocean representatives redescribed as *S. chupachups*.

Generally, molecular data for species reported to have a bipolar distribution are scarce but they are available for some taxa.

Bipolarity was examined in two diatom species: *Fragilariopsis cylindrus* and *F. nana*. Unfortunately difficulties persist in identifying these species, and although bipolarity was not confirmed, neither was it refuted.

Bipolarity has also been investigated in marine bacterial isolates. Using the mitochondrial gene, 16S rRNA, it has been shown that *Shewanella frigidimarina* occurs in the Southern Ocean (Prydz Bay) and the Arctic (Greenland Sea and Canada Basin). However, limited sampling means that this species may have a cosmopolitan distribution.

Mitochondrial COI gene sequences of the pteropod *Limacina helicina* from populations sampled in the Arctic and Southern Oceans were found to differ by

33.56 %, whilst genetic distance between individuals within each of these locations was very small (i.e. Arctic 0.15 %, Southern Ocean 0.60 %). This provides strong evidence that these are different species (Hunt et al. 2010).

Gene exchange between the poles, where no intermediate populations exist, is probably a rare phenomenon. Cosmopolitanism however, particularly amongst deep-sea species, is more likely. Although datasets do not yet exist, mostly because of the difficulties in obtaining widespread deep-sea samples, future molecular data may reveal global panmixia in some deep-sea cosmopolites, highlighting the deep-ocean connections between Antarctic waters and the rest of the globe.

3.4 Connectivity within the Southern Ocean

3.4.1 The Southern Ocean as a Biodiversity Hotspot

The Ecology of the Antarctic Sea-Ice Zone (EASIZ) programme strongly contributed to refuting the idea that the Southern Ocean was species poor (Clarke and Arntz 2006). Working on a shelf-species estimate of at least 4,100 species, Clarke (2008) concluded that the richness of the shelf fauna was comparable with that of Hawaii or north-west Europe. Following intensive taxonomic work during the Census of Marine Life, the number of known shelf species has risen to 5,800 (DeBroyer and Danis 2011), but recent molecular work suggests that many cryptic species are yet to be discovered and true estimates of Southern Ocean biodiversity will be very much higher.

3.4.2 Cryptic Species

Cryptic species have been reported in a diversity of taxa including amphipods (Lörz et al. 2009; Baird et al. 2011; Havermans et al. 2011), isopods (Leese and Held 2008), ostracods (Brandão et al. 2010), sea-spiders (Mahon et al. 2010; Krabbe et al. 2010), bivalves (Linse et al. 2007), sea slugs (Wilson et al. 2009), octopods (Allcock et al. 2011), brittle stars (Hunter and Halanych 2008), sea cucumbers (O'Loughlin et al. 2011), crinoids (Wilson et al. 2007), polychaetes (Schueller 2011) and nemerteans (Thornhill et al. 2008). These studies were all molecular based, and the majority of them employed the mitochondrial gene cytochrome oxidase I, the DNA barcoding gene. Most of these studies looked for (but did not always find) evidence of a "gap" range between the highest intra-specific and the lowest interspecific distances, or looked for breaks (based on a pre-determined threshold) in haplotype networks built using statistical parsimony or similar techniques. Brandão et al. (2010) employed a maximum likelihood

approach (Pons et al. 2006) to quantitatively search for species limits and it is likely that this method will be used more frequently in the future.

Almost all studies revealing cryptic species have been based on mitochondrial sequence data which are therefore haploid and only representative of the female lineage. Some studies have included diploid markers. For example, Baird et al. (2011) included the nuclear gene ITS on a study of amphipods and found congruence with their mitochondrial data; Raupach et al. (2007) employed the nuclear gene 18S rRNA on a study of isopods and also found congruence with their mitochondrial data. Conversely neither the nuclear gene 28S rRNA in a brooding bivalve (Linse et al. 2007) nor the nuclear gene ITS in ostracods (Brandão et al. 2010) were found to be congruent with mitochondrial data derived from these species. Brandão et al. (2010) suggested that introgression or incomplete lineage sorting might account for the differences. Leese and Held (2008), in the first reported study using microsatellites on invertebrate species in the Southern Ocean, did find congruence with mitochondrial data.

For the most part, the presence of cryptic lineages appears to be associated with taxa with limited dispersal capacity. This suggests that connectivity around the Southern Ocean might have been limited for these taxa at certain times, presumably during glacial maxima when ice extents were at their peak and post glacial maxima where a lack of dispersal stage prevented the populations rapidly exchanging genes. Cryptic lineages have likely had limited time to diverge morphologically and are therefore probably indicative of recent speciation. This certainly fits with a theory of limited connectivity between populations during the last glacial maximum. If speciation was widespread as a result of glacial cycles, this helps explain why the Southern Ocean appears to be a biodiversity hotspot.

Interestingly, the inclusion of rarefaction curves in some studies has indicated an under sampling of genetic diversity (Wilson et al. 2009; Baird et al. 2011). In molecular ecology, rarefaction curves plot the discovery of new haplotypes against sampling effort and, as in their ecological application, tend towards an asymptote that indicates the number of haplotypes in the population. Routine inclusion of such analyses will likely suggest that the true number of cryptic species is higher than currently detected.

3.4.3 Eurybathy and Circumpolarity

While the presence of cryptic species suggests a lack of connectivity within the Southern Ocean, there may have been persistent and continued connectivity between widespread populations in some species. Eurybathy, having a distribution encompassing a wide depth range, and circumpolarity, having a distribution that encircles the Antarctic continental landmass, are two characteristics that have been widely reported for Southern Ocean species.

In some cases, molecular studies that have revealed the presence of cryptic lineages have shown species to be have more restricted depth and geographic

ranges than originally thought. Until recently, *Glycera kerguelensis*, a polychaete worm, was thought to inhabit depths ranging from around 150 m to deeper than 4,000 m. Molecular work has now shown this taxon comprises multiple cryptic species each with a much more restricted depth distribution (Schueller 2011). Nonetheless, molecular studies have confirmed extreme eurybathy in at least two species. An undescribed amphipod species in the genus *Abyssorchomene* has been confirmed as inhabiting depths from around 300 m to below 4,000 m (Havermans et al. 2011) while a single lineage of the pycnogonid *Nymphon australe* has been confirmed from 150 m to below 1,000 m (Arango et al. 2011). Whether this species extends to its reported depth of below 4,000 m awaits confirmation. Nonetheless, even the confirmed depth range would be unusual in temperate taxa.

Similarly, Hemery et al. (2012) recognised six 'phylogroups' within the crinoid 'species' *Promachocrinus kerguelensis,* which were all found to be circumpolar, sympatric and eurybathic. *P. kerguelensis* is known from 20 to 2,100 m depth and is likely to have a large dispersal potential due to its positively buoyant lecithotrophic larvae. The deeper shelf of the Antarctic continent and periodic glaciation (over Milankovitch cycles) reducing available benthic habitat on the shelf, coupled with the rise and fall of sea levels, may be natural evolutionary drivers towards eurybathy.

Geographically widespread distributions throughout the Southern Ocean are clearly less common than once thought and are most often associated with a pelagic dispersal stage (usually larval). For example analysis of two mitochondrial (16S rRNA, COI) and one nuclear (28S rRNA) gene fragments in two species of shrimps (*Chorismus antarcticus, Nematocarcinus lanceopes*) with planktotrophic larvae showed no evidence of cryptic speciation across a circum-Antarctic range (Raupach et al. 2010). Similarly, the limpet *N. concinna*, which is a broadcast spawner, has a widespread distribution but is probably restricted from circumpolarity by lack of suitable coastal habitat and the relatively short period (<4 weeks) of larval dispersal (González-Wevar et al. 2011). Population genetic studies using AFLPs and comparing *N. concinna* with the direct-developing top shell *Margarella antarctica* concluded that population structure reflected life history (Hoffman et al. 2011).

For many species, the mode of reproduction is not actually confirmed, but rather inferred from congeners or from egg size. An unlikely circum-Antarctic distribution in *Astrotoma agassizi*, a brittle star thought to lack a larval stage (Hunter and Halanych 2008), was later satisfactorily explained when a larval DNA barcoding (i.e., sequencing of the mitochondrial gene COI) programme identified a planktonic dispersive stage for this species (Heiemeyer et al. 2010). Elucidating life-history strategies through widespread DNA barcoding of zooplankton could yield much useful information on the life history strategies of Southern Ocean fauna.

It is likely that having a dispersive stage facilitates recolonisation of newly available habitat when ice shelves retreat following glacial maxima. If species do persist during glacial maxima in small refugia on the continental shelf then larvae would be rapidly distributed around the continent by ocean currents as soon as

warmer conditions prevailed. This process should leave a characteristic molecular signature that reflects a population bottleneck (low diversity) and population expansion. A star-like haplotype pattern would be predicted, with one to a few very abundant ancestral haplotypes and multiple haplotypes that differ only slightly and occur at low frequencies. Several examples of such a haplotype pattern have now been reported from the Southern Ocean, for example in the sea urchin *Sterechinus neumayeri* (Diaz et al. 2011) and in the shrimp *C. antarcticus* (Raupach et al. 2010). The latter study also detected a departure from mutation-drift equilibrium in the genetic signal—evidence of population expansion. Similar population expansions have been detected in krill (Goodall-Copestake et al. 2010) and the endemic Southern Ocean limpet *N. concinna* (González-Wevar et al. 2011) and may be indicative of population expansion following glacial maxima.

3.5 Summary and Future Directions for Molecular Work

In the Southern Ocean, with the exception of studies on vertebrates and commercially valuable species, molecular ecology and phylogenetics are in their infancy. Yet they are transforming our understanding of connectivity within the Southern Ocean itself, and between the Southern and other oceans. At least half the studies result from DNA barcode data, in most cases because of the collaboration between the Canadian Centre for DNA Barcoding at the University of Guelph with the Census of Antarctic Marine Life. This has provided momentum within the Antarctic research community. Future molecular ecology studies should focus on additional genes and markers, particularly nuclear markers, including microsatellite markers. To date, microsatellites have been developed for only a handful of invertebrate species: Antarctic krill *Euphausia superba* (Bortolotto et al. 2011), the serolid isopods *Septemserolis septemcarinata* (Leese et al. 2010) and *Ceratoserolis trilobitoides* (Held and Leese 2007; Leese and Held 2008), and three octopus species: *Pareledone turqueti* (Strugnell et al. 2009a, 2012), *P. charcoti* (Strugnell et al. 2009a) and *Adelieledone polymorpha* (Strugnell et al. 2009b).

Future molecular ecology studies should also include haplotype networks and look for network patterns that can be predicted under different refugial scenarios at glacial maxima. They should also look for congruent patterns between nuclear and mitochondrial markers and they should seek evidence for recent (post glacial maximum) population expansion in the molecular signatures. They may also be able to confirm that hypothesised historical seaways (Fig. 3.1) acted as a conduit for gene flow. Similarities in molecular data between the two areas have been noted (Linse et al. 2007; Strugnell et al. 2012), but more evidence is required.

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