



# Divergence between Antarctic and South American marine invertebrates: What molecular biology tells us about Scotia Arc geodynamics and the intensification of the Antarctic Circumpolar Current



Elie Poulin<sup>a</sup>, Claudio González-Wevar<sup>a,\*</sup>, Angie Díaz<sup>a,b</sup>, Karin Gérard<sup>a</sup>, Mathias Hüne<sup>a</sup>

<sup>a</sup> Laboratorio de Ecología Molecular, Instituto de Ecología y Biodiversidad, Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Las Palmeras #3425, Ñuñoa, Santiago, Chile

<sup>b</sup> Laboratorio de Macroalgas Antárticas y Subantárticas, Departamento de Ciencias y Recursos Naturales, Facultad de Ciencias, Universidad de Magallanes, Av. Bulnes # 01855, Punta Arenas, Chile

## ARTICLE INFO

### Article history:

Received 21 October 2013

Received in revised form 24 June 2014

Accepted 26 July 2014

Available online 9 August 2014

### Keywords:

mtDNA divergence

COI

Molecular clock hypothesis (MCH)

Central Scotia Sea

Middle Miocene climatic transition

ACC onset and intensification

## ABSTRACT

Continental drift processes such as major gateway openings have been historically advocated to explain the distribution of marine benthic taxa in the Southern Ocean (SO). The separation between Antarctic Peninsula and the southern tip of South America together with the onset of the Antarctic Circumpolar Current (ACC) represent the final step for the complete isolation of the Antarctic region. However, there is still controversy concerning the timing and mode of this process, and especially about the role of the Scotia Arc geodynamics in the development of a fully deep and intensified ACC circulation. Based on mitochondrial Cytochrome c Oxidase Subunit I (COI) sequences obtained from different taxa, we performed molecular comparisons between Antarctic and South American relatives to provide independent time estimations of Antarctica's isolation. We include in the analyses congeneric Antarctic and Patagonian near-shore marine benthic invertebrates including indirect developers (*Nacella*, *Yoldia*, *Sterechinus*, and *Parbolasia*) and brooders (*Xymenopsis* and *Trophonella*). Considering the levels of genetic differentiation between relatives from both regions and assuming the molecular clock hypothesis, we estimated the onset of their respective divergence. On one hand, similar levels of genetic distance in broadcast-spawners (7%–8.3%) support the hypothesis that the development of an effective barrier between Antarctica and South America occurred almost simultaneously for these groups. Divergence time estimations based on specific substitution rates indicate that the separation occurred near the Mio-Pliocene transition, long after the physical separation of both continents. Genetic distance and divergence time estimation in direct developers indicate an older separation time, close to the mid-Miocene. Even when the analyzed groups included both broadcast-spawners and brooder organisms, the divergence between Antarctic and South America lineages rather than being related to processes of continental drift, seems to be associated more to major changes in the Southern Ocean such as the evolution of the Scotia Arc and the deepening of the Drake Passage. Accordingly, these results support a genetic continuity between Antarctica and South America, probably along the Scotia Ridge, until the middle Miocene and a late ACC intensification at the Mio-Pliocene boundary.

© 2014 Elsevier B.V. All rights reserved.

## 1. Introduction

The Southern Ocean (SO) covers about  $34.8 \times 10^6$  km<sup>2</sup>, which represents a 8% of the world's ocean surface and is considered as a major driver of global oceanic circulation playing an essential role in deep-sea water formation and circulation (Rintoul et al., 2001). This ocean includes all water masses south of the Polar Front, a well-defined circum-Antarctic oceanographic area that marks the northernmost extent of

cold surface waters (Aronson et al., 2007). This vast region harbors a significant part of the planet's marine diversity (~5%; Gutt et al., 2004; Barnes and Peck, 2008). The distribution, abundance and composition of its marine benthic fauna reflect the interaction of geological, climatic, oceanographic and biotic elements operating since the Mesozoic (Crame, 1997, 1999; Griffiths et al., 2009; Clarke and Crame, 2010; Allcock and Strugnell, 2012). According to Knox and Lowry (1977) the SO continental shelf faunal communities comprise taxa of different origins including: (a) relict endemic "formed in the place where found" fauna which has evolved in situ; (b) groups of taxa derived by migration into shallow water from adjacent deep-sea basins; and (c) a fauna that dispersed into Antarctica from South America along the islands of the Scotia Ridge. More recently, Clarke (2008) recognized a fourth

\* Corresponding author at: Laboratorio de Ecología Molecular, Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Las Palmeras # 3425, Ñuñoa, Santiago, Chile.

E-mail address: [omeuno01@hotmail.com](mailto:omeuno01@hotmail.com) (C. González-Wevar).

component including taxa that migrated in the opposite direction, from Antarctica to South America, through the Scotia Arc. Many groups of marine organisms that are successful and diverse in adjacent areas are scarcely represented or even absent in the Southern Ocean (Crame, 1999; Aronson and Blake, 2001). However, other marine groups including Porifera, Bryozoa, Echinodermata, Polychaeta, Ascidiacea, Pycnogonida, Amphipoda and Isopoda are highly abundant and diverse in the SO, suggesting that major climatic and oceanographic changes in the region did not impede their evolutionary success (Clarke and Crame, 1989; Clarke et al., 1992; Clarke, 1996; Linse et al., 2006; Aronson et al., 2007; Rogers, 2007). Mackensen (2004) recognized three main periods that dramatically affected the biogeography in the SO. The first one during the Eocene/Oligocene boundary (~34 Ma) matches with the onset of the Antarctic isolation through the opening of major oceanic gateway and the initiation of the Antarctic Circumpolar Current (ACC; Zachos et al., 2001; Barker and Thomas, 2004; Livermore et al., 2005; Pfuhl and McCave, 2005). A second period occurred during the middle Miocene ~14 Ma is associated to an increased southern bottom water formation, an intensification of the ACC and the re-establishment of an ice sheet on East Antarctic and along the Pacific margin of West Antarctica (Lawver et al., 2003; Verducci et al., 2009). Finally, the Quaternary is another period of biogeographic changes in the SO because it is characterized by the alternation between glacial and interglacial periods that greatly affected seasonality and intensity of sea-ice formation in the region and latitudinal changes in the position of the ACC (Barker and Thomas, 2004; Gersonde et al., 2005; Kemp et al., 2010). As stated above, the opening of the Tasman gateway and the Drake Passage shaped past and present oceanographic circulation in the region (Barker et al., 2007). The ACC represents the major current system in the planet (Orsi et al., 1995) flowing eastward around Antarctica and is delimited by two main boundaries, the Polar Front (APF) and the sub-Antarctic Front (SAF; Rintoul et al., 2001; Barker et al., 2007). The positions of these fronts have major biogeographic implications for the biota in the Southern Ocean (Lawver et al., 2003; Linse et al., 2006; Strugnell et al., 2008; Griffiths et al., 2009, 2011; Pierrat et al., 2013). Few epipelagic species, with the exception of marine mammals and birds, are distributed both inside and outside the APF (Aronson et al., 2007). Accordingly, the ACC represents an important biogeographic barrier for many invertebrate taxa between Antarctic and sub-Antarctic areas (Shaw et al., 2004; González-Wevar et al., 2010, 2012a, b). However, the ACC also constitutes an important carrier of organisms between geographically distant sub-Antarctic areas, especially for those species with high dispersive potential (Beu et al., 1997; Page and Linse, 2002; Thorpe et al., 2004; Waters, 2008; Fraser et al., 2009; Leese et al., 2010; Macaya and Zuccarello, 2010a; Díaz et al., 2011). Together with the tectonic and oceanographic changes, climate shift has exerted a major role in the region, shaping abundance, structure and distribution of the SO biota (Clarke and Crame, 1989, 2010; Clarke et al., 1992; Aronson et al., 2007; Clarke, 2008). These changes influenced levels of endemism and isolation from, in addition to conductivity to the world's ocean basins (Clarke et al., 2005; Strugnell and Allcock, 2013).

A high level of faunal affinities has been described between Antarctica and the southern tip of South America, commonly known as the “Antarctic–Magellan Connection” (Arntz, 1999; Brandt et al., 1999; Arntz et al., 2005; Thatje et al., 2005). The accepted explanation for such affinity relies on the fact that these continents were contiguous until the opening of the Drake Passage and were progressively separated by deep waters (Crame, 1999), two processes that are closely related to the geodynamic evolution of the Scotia Arc. On one hand, even when the Drake Passage is apparently too deep to allow dispersal of shelf benthic organisms (Shaw et al., 2004; Hunter and Halanyc, 2008), some nominal species are reported in both Antarctica and southern South America (i.e. *Yoldia eightisii*, *Kerguelenella lateralis*, *Promachocrinus kerguelensis*, *Parbolasia corrugatus*). On the other hand, several marine organisms from different provinces of the SO such as *Euphausia*

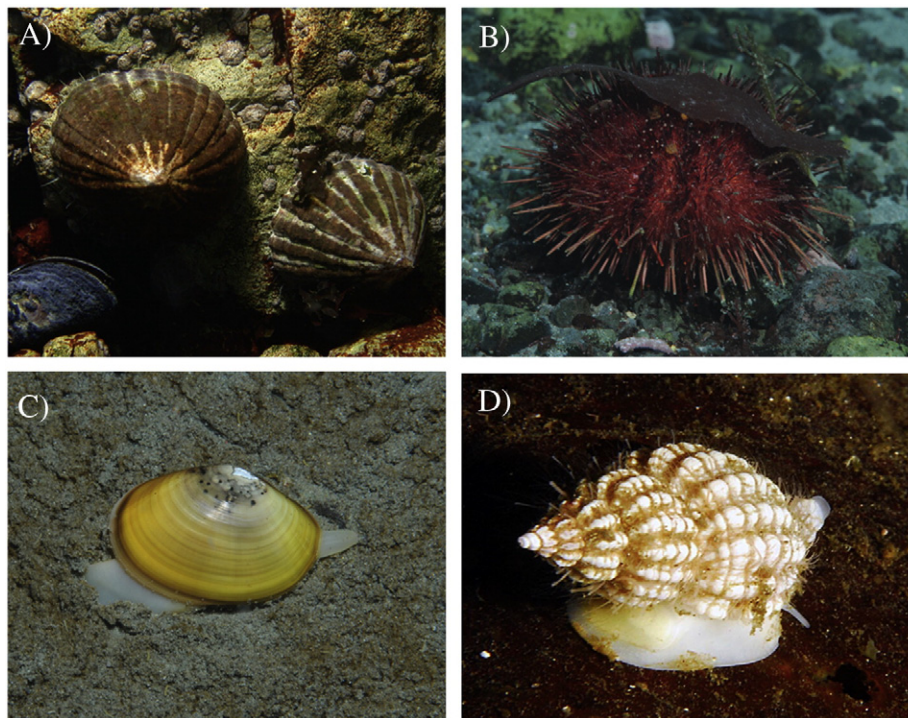
(Patarnello et al., 2007), and fishes (Clarke and Johnston, 1996; Waters et al., 2000) exhibit a high degree of genetic differentiation, supporting the hypothesis that their respective separations followed the rhythms and trends of continental drift processes. Nevertheless, recent molecular data in several marine invertebrate taxa, especially in those with dispersive capacity have shown that their divergences are much younger than the physical separation of the SO continental landmasses. These studies provide new evidence of the importance of long-distance dispersal in the biogeography of the Southern Ocean (Helmuth et al., 1994; Coyer et al., 2001; Page and Linse, 2002; Fraser et al., 2009; Macaya and Zuccarello, 2010b; Díaz et al., 2011) or of recent climatic/oceanographic processes among SO provinces (González-Wevar et al., 2010, 2012a,b, submitted for publication; Hüne et al., submitted for publication). Moreover, the presence of non-Antarctic anomuran and brachyuran larval stages at King George Island, South Shetland Islands, Antarctic Peninsula (Thatje and Fuentes, 2003) has been advocated as evidence that some groups of nearshore marine organisms may travel across the APF (Tavares and De Melo, 2004; Clarke et al., 2005). Such findings highlight the permeability of the Polar Front in space and time, raising questions about the isolation of Antarctica, how organisms got to this continent and how often these processes happened in the past.

In this study we performed DNA comparisons between related Antarctic and South American marine organisms from different invertebrate phyla (Fig. 1). The information contained in their DNA sequences will permit us to estimate rhythms and trends in the biogeography of marine benthic nearshore organisms between these provinces of the Southern Ocean. Moreover, in relation to the dispersal capacity of each group, we will estimate when Antarctica and the southern tip of South America were effectively separated.

## 2. Material and methods

We analyzed a fragment of the mitochondrial gene Cytochrome c Oxidase Subunit I (COI) in marine invertebrates with indirect development and at different taxonomic levels. For this, we included in the analyses Antarctic and South American congeneric species of the sea urchin *Sterechinus* (945 bp; Díaz et al., 2011) and the patellogastropod *Nacella* (662 bp; González-Wevar et al., 2011a, 2012b; Fig. 1). Similarly, we included sequences of Antarctic and Patagonian populations of the nominal species *Parbolasia corrugatus* (nemertean; Thornhill et al., 2008), and of the bivalve *Y. eightisii* (González-Wevar et al., 2012a; Fig. 1). Finally, we included in the analyses Antarctic and South American COI sequences of the direct developer *Trophonella* (Antarctica) and its Patagonian relative *Xymenopsis muriciformis*.

Specimens of the Antarctic limpet *Nacella concinna* were collected from five localities along the western Antarctic Peninsula (González-Wevar et al., 2011b; accession numbers ACCN: KFP261314–KFP261330) and *Nacella magellanica* specimens included individuals from three localities in Patagonia (ACCN: JX262742–JX262778; González-Wevar et al., 2012b). Similarly, *Sterechinus neumayeri* individuals were sampled from two localities of the western Antarctic Peninsula (Fildes and Covadonga Bay, King George Island, South Shetland Islands) while *Sterechinus agassizii* collected in the Argentinean continental shelf, Patagonia (Díaz et al., 2011). Individuals of *Trophonella* sp. were collected at Fildes Bay, King George Island, South Shetland Islands and individuals of *Xymenopsis muriciformis* were collected in Punta Santa Ana, Strait of Magellan. We also included in the analyses five individuals of *Y. eightisii* collected in Fildes Bay, King George Island, South Shetland Islands, and five specimens from Porvenir Bay, Strait of Magellan. Finally, and for comparison purposes, we included *P. corrugatus* sequences from Antarctic Peninsula (ACCN: EU194803.1, EU194804.1, EU194806.1, EU194805.1) and the Argentinean Patagonian coast (ACCN: EU194817.1, EU194816.1, EU194815.1, EU194819.1, EU194818.1, EU194817.1; Thornhill et al., 2008).



**Fig. 1.** Near-shore marine invertebrates from South America: A) *Nacella magellanica* (Strait of Magellan); and Antarctica: B) *Sterechinus neumayeri* (Fildes Bay, King George Island); C) *Yoldia eightsii* (Fildes Bay, King George Island); D) *Trophonella* sp. (Fildes Bay, King George Island). Photograph A) courtesy of César Cárdenas; B) & C) courtesy of Dirk Schories, and D) Sebastian Rosenfeld.

The selected molecular marker (mtDNA COI) was amplified in new specimens of *Trophonella*, and *Xymenopsis* using the universal primers described by Folmer et al. (1994). Amplicons were purified and sequenced in both directions by Macrogen Inc. (South Korea). Sequences were edited with Proseq 2.91 (Filatov, 2009) and aligned using Clustal W (Thompson et al., 1994). Finally, unpublished COI sequences of *Sterechinus* (ACCN: KJ571168–KJ571197), *Yoldia* (ACCN: KJ571165–KJ571167), *Xymenopsis* (ACCN: KJ571163–KJ571164), and *Trophonella* (ACCN: KJ571160–KJ571162) were deposited in GenBank.

We estimated the average number of nucleotide substitutions and calculated the pairwise percent of divergence (uncorrected p-distances) between Antarctic and South American lineages of the analyzed groups. We determine whether the evolutionary rate was constant in the different analyzed taxa using a likelihood ratio test (Felsenstein, 1981) in DAMBE (Xia and Xie, 2001). Once the constancy of the evolutionary rate was confirmed in each of the included groups we performed divergence time estimations between Antarctic and South American lineages using a strict Molecular Clock Hypothesis (MCH) and specific substitution rates (Table 1). The MCH assumes that DNA and protein sequences evolve at a constant rate through

time for a given lineage and therefore the genetic difference between any two species is proportional to the time since they last shared a common ancestor (Bromham and Penny, 2003).

Finally, we constructed Median-joining genealogical relationships between Antarctic and South American in Network 4.6 using the default parameters of the software (<http://www.fluxus-engineering.com>). This method allows simple reconstructions of phylogenies based on intra-specific genetic data such as mitochondrial DNA variation (Bandelt et al., 1999; Posada and Crandall, 2001).

### 3. Results

Major genetic divergences were detected between Antarctic and South American lineages here included (Table 1). For instance, congeneric *Sterechinus* species from Antarctica and South America showed 7.2% of differences (Fig. 2A). Likewise, congeneric *Nacella* species from Antarctica and South America exhibited a 7.7% of difference (Fig. 2B). The species *Y. eightsii* from Antarctica and Patagonia exhibited a 7.0% of divergence (Fig. 2C). Similarly, the species *P. corrugatus* from Antarctica and Patagonia exhibited 8.3% of divergence (Fig. 2D). Finally,

**Table 1**  
Percentage sequence divergence (uncorrected p distance), substitution rates, and divergence time estimations between Antarctic and South American lineages of marine benthic invertebrates.

Taxa	Pairwise percent divergence	Substitution rate	Reference	Divergence time estimations (Ma)
<i>S. neumayeri</i> vs. <i>S. agassizi</i>	7.0	0.51–0.72	Lee et al. (2004)	4.4–5.0
<i>N. concinna</i> vs. <i>N. magellanica</i>	7.7	1.0	González-Wevar et al. (2011a,b) and González-Wevar et al. (2012a,b)	3.7
<i>Trophonella</i> vs. <i>Xymenopsis</i>	10.9	0.4	Wares and Cunningham (2001)	13.6
<i>Parbolasia corrugatus</i>	8.3	Not available	Thornhill et al. (2008), based on Wares and Cunningham (2001)	4.2–14.5
<i>Yoldia eightsii</i>	7.2	0.95	Wares and Cunningham (2001)	3.9
<i>Astrotoma</i>	6.8	3.1–3.5	Hunter and Halanych (2008) based on Lessios et al. (1999)	1 Ma
<i>Odontaster</i>	6.7	3.1–3.5	Janosik et al. (2011) based on Lessios et al. (1999)	1 Ma

muricids from Antarctica (*Trophonella*) and South America (*Xymenopsis*) showed a 10.9% of divergence (Fig. 2E).

Considering specific substitutional rates, divergence time estimations between Antarctic and South American lineages suggest that the separation in the analyzed groups range between the late mid-Miocene and Pliocene (13.6–3.7 Ma; Fig. 3). The last contact between *S. neumayeri* and *S. agassizi* occurred around 4.4 and 5.0 Ma. The separation between *N. concinna* and *N. magellanica* took place ~3.7 Ma while the separation between Antarctic and South American *Y. eightsii* occurred ~3.9 Ma (Fig. 3). Unfortunately, no substitution rate is available for Nemertea and divergence date between *P. corrugatus* from Antarctica and South America could not be estimated. Thornhill et al. (2008), using substitution rate of third position sites in COI from non-anthropozoan invertebrate groups, estimated a divergence between 4.2 and 14.5 Ma between Antarctic and South American populations of this species. Indirect developers like *Nacella*, *Sterechinus*, *Parbolasia*, and *Yoldia* showed younger divergence than the brooder species here included. In the case of Antarctic *Trophonella* and South American *Xymenopsis*, divergence time estimations indicate an older separation during the mid-Miocene (~13.6 Ma).

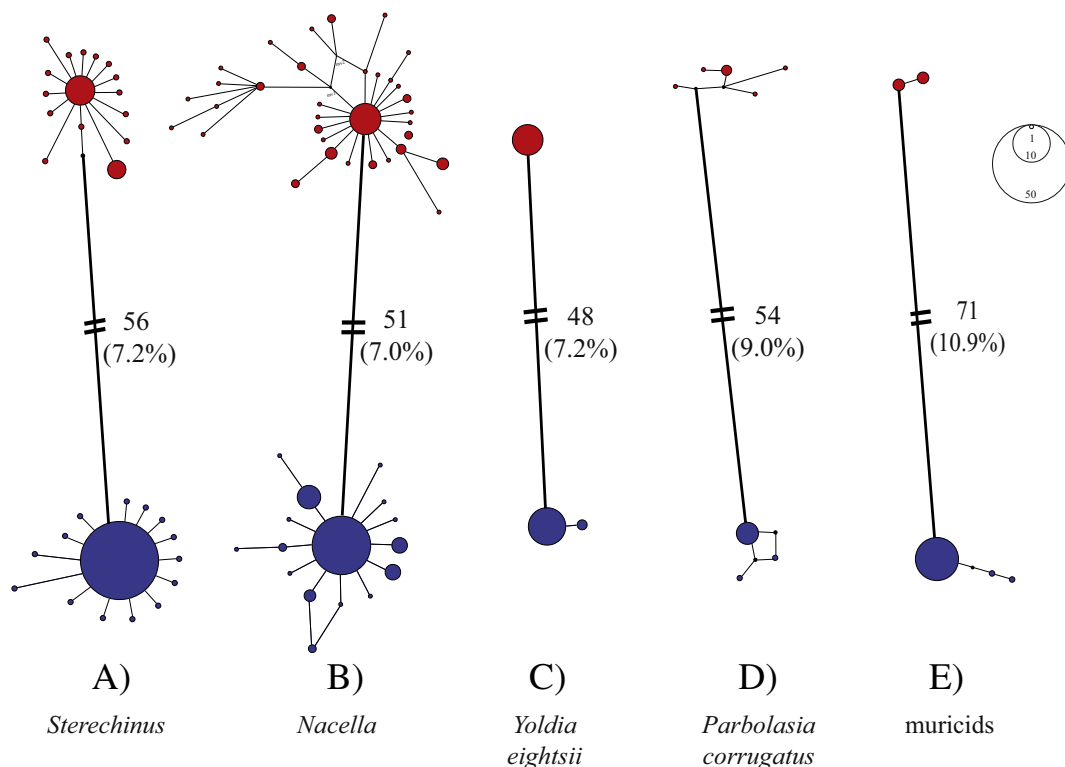
#### 4. Discussion

Molecular and analytical procedures have renewed the interest in biogeographical studies, particularly in the Southern Ocean (Linse et al., 2006; Griffiths et al., 2009, 2011; González-Wevar et al., 2010; Díaz et al., 2011; Downey et al., 2012; Pierrat et al., 2013). The inclusion of different sources of data such as paleogeographical, paleoclimatic and paleoecological evidence allow the formulation of new biogeographical interpretations in a more precise historical framework (Lomolino et al., 2006; Pearse et al., 2009). This can lead to a better understanding of the role of climate shifts and oceanography in shaping evolutionary processes in the Southern Ocean (Griffiths et al., 2009; Pierrat et al., 2013).

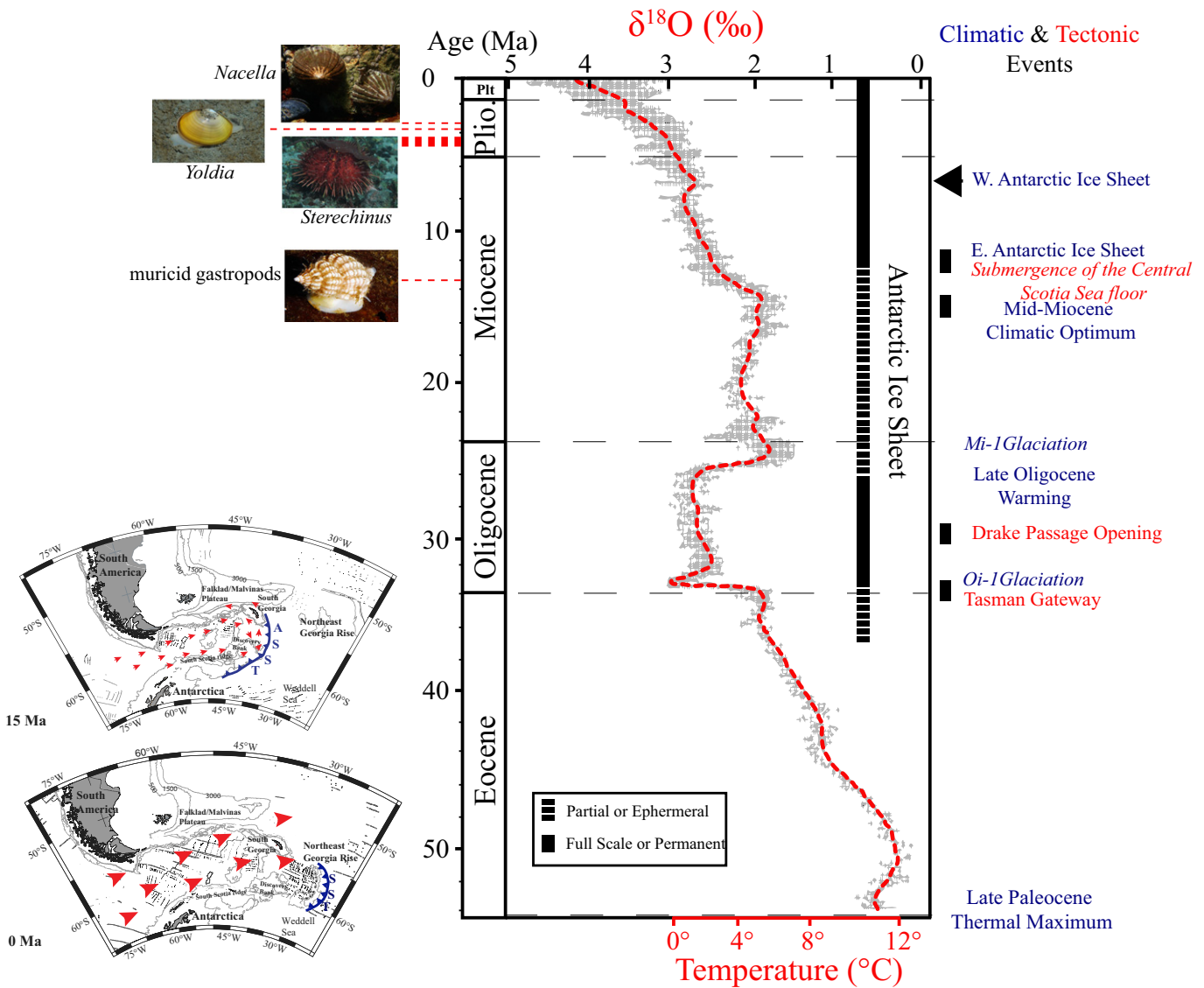
Molecular comparisons in this study recognized marked genetic dissimilarities between Antarctic and South American lineages belonging to Mollusca, Echinodermata and Nemertea. In each one of them, we recognized similar evolutionary trajectories suggesting that Antarctic and South American lineages constitute complete different Evolutionary Units separated for several million years. Accordingly, the ACC seems to represent an efficient biogeographic barrier in these groups of broadcast-spawners since the mid-Miocene to the early Pliocene.

Since its proposal, the Molecular Clock Hypothesis has provided an insight into the mechanisms of molecular evolution and constitutes an important tool in many areas of evolutionary biology, systematic, conservation genetics and molecular ecology (Bromham and Penny, 2003; Kumar, 2005; Ho, 2008). This hypothesis provides a simple and useful method to estimate evolutionary timescales, especially for those organisms that have left few traces of their biological history in the fossil record (Ho, 2008). However, these clocks sometimes behave in an erratic manner, which have raised questions about their use, particularly when assuming the same substitution rate across different taxa (Ayala, 1997). In this regard, in this study we used specific substitution rates for each of the analyzed group. According to Bromham and Penny (2003) even an approximate clock allows time estimates of events in evolutionary history, which in turn provides a method for testing a wide range of biological hypothesis.

Divergence time estimations derived from this study indicate that the effective separation between Antarctic and South American taxa, especially for groups with dispersive potential, occurred between 3.7 and 14.5 Ma, long after the physical separation of these continents estimated between 41 Ma (Livermore et al., 2005) and 23.9 Ma (Eagles and Livermore, 2002; Pfuhl and McCave, 2005; Scher and Martin, 2006; Lyle et al., 2007), and to the initiation of the ACC. Such divergence time estimations are consistent with recent molecular studies in notothenioid fishes where the most speciose clades in this suborder (*Trematomus*, Channichthyidae, and Artedidraconidae) originated



**Fig. 2.** Median-joining haplotype networks constructed using COI sequences from Antarctic (blue) and Magellanic (red) taxa. A) *Sterechinus* (n = 150), B) *Nacella* (n = 191); C) *Yoldia eightsii* (n = 20); D) *Parbolasia corrugatus* (n = 20); E) muricid gastropods (n = 20). A circle represents each haplotype and its size is proportional to its frequency. Pairwise divergence sequences (uncorrected p-distances) between Antarctic and South American lineages are included.



**Fig. 3.** Divergence time estimations between Antarctic and South American marine related taxa based on mtDNA sequences. Global deep-sea oxygen isotope records and temperatures based on data compiled from more than 40 DSDP (modified from Zachos et al., 2001) associated to major climatic and tectonic processes in the region. Scheme of the tectonic setting of the Scotia arc region is shown together with main oceanic flows before the genetic divergence onset (mid-Miocene 15 Ma) and present day (modified from Dalziel et al., 2013a). Size of the arrows (red) indicates the intensity of the ACC jets. Where ASST = ancestral South Sandwich Trench, SST = South Sandwich Trench.

between 11.6 and 5.3 Ma, more than 10 Ma after the origin of the group (Near et al., 2012). Similarly, the separation between Antarctic and sub-Antarctic notothenioid genera ranged between 9 Ma (Bargelloni et al., 2000) and 6.1 Ma (Stankovich et al., 2002) following the onset of intensified cooling conditions in the SO (Near et al., 2012). The divergence between the Antarctic bivalve *Limatula ovalis* and its sub-Antarctic relative *Limatula pygmae* indicate a separation between 8.03 and 5.79 Ma (Page and Linse, 2002) and the separation between Antarctic and sub-Antarctic populations of the crinoid *P. kerguelensis* suggest a split between 3.75 and 4.24 Ma (Wilson et al., 2007). Levels of pairwise percent divergence (uncorrected p-distances) between Antarctic and South American population of *Astrotoma* (6.8%; Hunter and Halanych, 2008) and *Odontaster* (6.7%; Janosik et al., 2011) are similar to those reported here for *Nacella* (7.7%), *Sterechinus* (7.0%), and *Yoldia* (7.2%). In summary, numerous studies between Antarctic and sub-Antarctic invertebrate groups indicate that the separation of the marine benthic organisms in the region occurred near the Mio-Pliocene boundary. Accordingly, the onset of divergence among these taxa does not appear to have been a direct consequence

of the continental drift processes occurred in the region since the Mesozoic.

An explanation for the incongruence between the Antarctic–South America molecular divergence estimations and the expected separation based on the continental drift processes may rely in the fact that, even in allopatry (geographically separated), populations from Antarctica and South America could have maintained connectivity after the physical separation of the continental landmasses through passive dispersal of pelagic larval stages or rafting. As a matter of fact, such connectivity between geographically disjoint populations is a common feature among marine organisms with indirect development and has been recorded over much wider stretches of ocean than the geographic distance between the southern tip of South America and the Antarctic Peninsula (Jablonski, 1986; Jokiel, 1990; Cowen and Sponaugle, 2009; Gillespie et al., 2012). Finally, the disruption of connectivity among Antarctic and southern South America seems to be related to more recent climatic/oceanographic changes that followed the Middle Miocene Climatic Transition (MMCT). In this context, the installation of an effective barrier between Antarctic and South American faunas could be a

consequence of the intensification of the ACC. After MMCT, Sea Surface Temperatures (SST), salinity, and ice-volume trends support the occurrence of major changes in ocean circulation that triggered global cooling and the initiation of sub-zero polar conditions in the SO (Shevenell et al., 2004; Lewis et al., 2008). A gradual decrease of the SST is consistent with an intensification of the ACC (Verducci et al., 2009), a process also supported by different sources of data including strengthening of the westerly winds, atmospheric circulation shifts,  $\delta^{18}\text{O}$  signatures (Flower and Kennett, 1994; Heinrich et al., 2011), and by faunal isotopic changes at the Kerguelen Plateau (Verducci et al., 2009) and at continental Antarctica (Lewis et al., 2008). Moreover, recent studies in the Central Scotia Sea suggest that a remnant now-submerged volcanic arc may have formed a barrier to deep eastward oceanic circulation until after the mid-Miocene (Dalziel et al., 2013a). Hence, the full development of a deep ACC was not achieved until this period and may have played a significant role in the subsequent Southern Ocean cryosphere expansion (Lear et al., 2000; Zachos et al., 2001), to the strengthening of the westerly winds (Flower and Kennett, 1994; Shevenell et al., 2004), and to the ultimate separation between the Antarctic and the South America benthos.

In brooders (muricid gastropods), the onset of divergence is also much younger than the major tectonic processes that separated both continents. In the absence of dispersive larval stage, the persistence of a now submerged volcanic arc along the central Scotia Sea after the mid-Miocene (Dalziel et al., 2013a, 2013b) may have acted as a bridge between Antarctic Peninsula and Southern South America following a stepping stone model of dispersion. Alternatively, the absence of larval stage is not necessarily associated with low dispersal capacity. Many groups of brooding invertebrates exhibit a high degree of connectivity at large geographical scales in the SO, mainly through rafting (Helmuth et al., 1994; Leese et al., 2010; Nikula et al., 2010; Haye et al., 2012) or through mobile hosts (Domaneschi et al., 2002; Barnes et al., 2006; Gillespie et al., 2012). An older divergence between Antarctic and South American muricid gastropods (brooders) compared to the ones estimated for broadcast-spawners should be considered with prudence. Such differences were mainly related to lower substitution rates used in muricids rather than a noticeably higher percentage of sequence divergence (Table 1).

Even though some of the analyzed taxa are currently recognized as the same nominal species in Antarctica and South America (i.e. *Y. eightsii* and *P. corrugatus*), the molecular divergence between populations from these continents raises questions about their respective taxonomies. In fact, several studies in the Southern Ocean have demonstrated the existence of genetically distinct species that have not previously been distinguished morphologically (cryptic speciation) in the Southern Ocean (Held and Wägele, 2005; Raupach and Wägele, 2006; Allcock et al., 2011). These studies have encompassed a wide variety of invertebrate taxa such as ostracods (Brandão et al., 2010), amphipods (Baird et al., 2011; Havermans, 2011), isopods (Raupach et al., 2007; Leese et al., 2008), sea spiders (Krabbe et al., 2010), nemertean (Thornhill et al., 2008; Mahon et al., 2009), bivalves (Linse et al., 2007), octopods (Allcock et al., 2011), crinoids (Wilson et al., 2007), and nudibranchs (Wilson et al., 2009). Following this, cryptic speciation seems to represent a common evolutionary process in the Southern Ocean and a plausible explanation for the high degree of divergence detected between Antarctic and South American populations of the nominal species *P. corrugatus* (Thornhill et al., 2008) and *Y. eightsii*. In this respect, the islands of the Scotia Ridge seem to have played a crucial role in the evolution of the Southern Ocean marine benthos (Linse et al., 2007). These islands represent a biodiversity hotspot, considering that they constitute the northernmost distribution of many Antarctic marine invertebrate species, as well as the southernmost distribution for many South American ones. Further studies should attempt to elucidate the phylogenetic affinities of Scotia Arc benthos to understand the role of geodynamic and oceanographic changes in this region on the speciation processes involved

in the separation of Antarctic and South American shallow benthic fauna.

In conclusion, this study presents new information about the patterns of genetic differentiation between marine organisms of Antarctica and southern South America. The separation between lineages of these provinces of the Southern Ocean occurred during the Mio-Pliocene, long after the physical separation of these continents. In this scheme, the geodynamic evolution of Scotia Arc, and particularly the establishment of a full deep ACC after the cessation of central Scotia Sea arc activity and its submergence (Dalziel et al., 2013a,b), may represent a major driver of the isolation of marine Antarctic fauna. Accordingly, particular geologic processes in the Scotia Arc may be responsible for major oceanographic and climatic changes that generated the current biogeographic patterns observed in the marine fauna of the SO continental shelves.

## Acknowledgments

This study was supported by the following projects and institutions: Thesis projects INACHB\_01\_07, INACH Office ProjectG\_04\_11, CONICYT24090009, CONICYT Ph.D. D-21060218 and post-doctorate 3120075 to C.G-W; FONDECYT post-doctorate 3100139 to K.G; INACHD\_05-09 and CONICYT Ph.D. D\_21-08 to A.D. At the same time, this research was supported by the Projects P05-002 ICM and PFB 023 (Instituto de Ecología y Biodiversidad IEB, Universidad de Chile), INACH02-02, INACH13-05, and ECOSCO6B02 to E.P. Thanks are also due to international program as AntEco, CAML, EBA-SCAR and PROSUL—Brazil for encouraging and supporting Antarctic research in evolution.

## References

- Allcock, A., Strugnell, J., 2012. Southern Ocean diversity: new paradigms from molecular ecology. *Trends Ecol. Evol.* 27, 520–528.
- Allcock, A., Barratt, I., Eléaume, M., Linse, K., Norman, M., Smith, P., Steinke, D., Stevens, D.W., Strugnell, J.M., 2011. Cryptic speciation and the circumpolarity debate: a case study on endemic Southern Ocean octopuses using the COI barcode of life. *Deep-Sea Res. II Top. Stud. Oceanogr.* 58, 242–249.
- Arntz, W., 1999. Magellan–Antarctic: ecosystems that drifted apart. *Sci. Mar.* 63, 503–511.
- Arntz, W., Thatje, S., Gerdes, D., Gili, J., Gutt, J., Jacob, U., Montiel, A., Orejas, C., Teixidó, N., 2005. Antarctic–Magellan connection: macrobenthos ecology on the shelf upper slope, a progress report. *Sci. Mar.* 63, 237–269.
- Aronson, R., Blake, D., 2001. Global climate and the origin of modern benthic communities in Antarctica. *Am. Zool.* 41, 27–39.
- Aronson, R., Thatje, S., Clarke, A., Peck, L., Blake, D., Wilga, C., Seibel, B., 2007. Climate change and invisibility of the Antarctic benthos. *Annu. Rev. Ecol. Syst.* 38, 129–154.
- Ayala, F.J., 1997. Vagaries of the molecular clock. *Proc. Natl. Acad. Sci. U. S. A.* 94, 7776–7783.
- Baird, H.P., Miller, K.J., Stark, J.S., 2011. Evidence of hidden biodiversity, ongoing speciation and diverse patterns of genetic structure in giant Antarctic amphipods. *Mol. Ecol.* 20, 3439–3454.
- Bandelt, H., Forster, P., Röhl, A., 1999. Median-joining networks for inferring intraspecific phylogenies. *Mol. Biol. Evol.* 16, 37–48.
- Bargelloni, L., Marcato, S., Zane, L., Patarnello, T., 2000. Mitochondrial phylogeny of Notothenioids: a molecular approach to Antarctic fish evolution and biogeography. *Syst. Biol.* 49, 114–129.
- Barker, P., Thomas, E., 2004. Origin, signature and palaeoclimatic influence of the Antarctic Circumpolar Current. *Earth Sci. Rev.* 66, 143–162.
- Barker, P., Filippelli, G., Florindo, F., Martin, E., Scher, H., 2007. Onset and role of the Antarctic Circumpolar Current. *Deep-Sea Res. II Top. Stud. Oceanogr.* 54, 2388–2398.
- Barnes, D., Peck, L., 2008. Vulnerability of Antarctic shelf biodiversity to predicted regional warming. *Clim. Res.* 37, 149–163.
- Barnes, D., Hodgson, D., Convey, P., Allen, C., Clarke, A., 2006. Incursion and excursion of Antarctic biota: past, present and future. *Glob. Ecol. Biogeogr.* 15, 121–142.
- Beu, A., Griffin, M., Maxwell, P., 1997. Opening of Drake Passage gateway and Late Miocene to Pleistocene cooling in Southern Ocean molluscan dispersal: evidence from New Zealand and Argentina. *Tectonophysics* 281, 83–97.
- Brandão, S.N., Sauer, J., Schön, I., 2010. Circumantarctic distribution in Southern Ocean benthos? A genetic test using the genus *Macroscapha* (Crustacea, Ostracoda) as a model. *Mol. Phylogenet. Evol.* 55, 1055–1069.
- Brandt, A., Linse, K., Mühlenhardt-Siegel, U., 1999. Biogeography of Crustacea and Mollusca of the Subantarctic and Antarctic regions. *Sci. Mar.* 63, 383–389.
- Bromham, L., Penny, D., 2003. The modern molecular clock. *Nat. Rev. Genet.* 4, 216–222.
- Clarke, A., 1996. Benthic marine habitats in Antarctica. *Antarct. Res. Ser.* 70, 123–133.
- Clarke, A., 2008. Antarctic marine benthic diversity: patterns and processes. *J. Exp. Mar. Biol. Ecol.* 366, 48–55.

- Clarke, A., Crame, J., 1989. The origin of the Southern Ocean marine fauna. *Geol. Soc. Lond.* 47, 253–268.
- Clarke, A., Crame, J., 2010. Evolutionary dynamics at high latitudes: speciation and extinction in polar marine faunas. *Phil. Trans. R. Soc. B* 365, 3655–3666.
- Clarke, A., Johnston, I., 1996. Evolution and adaptive radiation of Antarctic fishes. *Trends Ecol. Evol.* 11, 212–218.
- Clarke, A., Crame, J., Stromberg, J., Barker, P., 1992. The Southern Ocean benthic fauna and climate change: a historical perspective [and discussion]. *Phil. Trans. R. Soc. B* 338, 299–309.
- Clarke, A., Barnes, D., Hodgson, D., 2005. How isolated is Antarctica? *Trends Ecol. Evol.* 20, 1–3.
- Cowen, R., Sponaugle, S., 2009. Larval dispersal and marine population connectivity. *Annu. Rev. Mar. Sci.* 1, 443–466.
- Coyer, J., Smith, G., Andersen, R., 2001. Evolution of *Macrocystis* spp. (Phaeophyceae) as determined by ITS1 and ITS2 sequences. *J. Phycol.* 37, 574–585.
- Crame, J., 1997. An evolutionary framework for the polar regions. *J. Biogeogr.* 24, 1–9.
- Crame, J., 1999. An evolutionary perspective on marine faunal connection between southernmost South America and Antarctica. *Sci. Mar.* 63, 1–14.
- Dalziel, I., Lawver, L., Pearce, J., Barker, P., Hastie, A., Barfod, D., Schenke, H., Davis, M., 2013a. A potential barrier to deep Antarctic circumpolar flow until the late Miocene? *Geology* 41, 947–950.
- Dalziel, I.W.D., Lawver, L.A., Norton, I.O., Gahagan, L.M., 2013b. The Scotia Arc: genesis, evolution, global significance. *Ann. Rev. Earth Planet. Sci.* 41, 767–793.
- Díaz, A., Feral, J., David, B., Saucède, T., Poulin, E., 2011. Evolutionary pathways among shallow and deep-sea echinoids of the genus *Sterechinus* in the Southern Ocean. *Deep-Sea Res. II Top. Stud. Oceanogr.* 58, 205–211.
- Domaneschi, O., Da Silva, J.R.M.C., Neto, L.R.P., Passos, F.D., 2002. New perspectives on the dispersal mechanisms of the Antarctic brooding bivalve *Mysella charcoti* (Lamy, 1906). *Polar Biol.* 25, 538–541.
- Downey, R., Griffiths, H., Linse, K., Janussen, D., 2012. Diversity and distribution patterns in high southern latitude sponges. *PLoS ONE* 7, e41672.
- Eagles, G., Livermore, R., 2002. Opening history of Powell Basin, Antarctic Peninsula. *Mar. Geol.* 185, 1–11.
- Felsenstein, J., 1981. Evolutionary trees from DNA sequences: A maximum likelihood approach. *J. Mol. Evol.* 17, 368–376.
- Filatov, D., 2009. Processing and population genetic analysis of multigenic datasets with ProSeq3 software. *Bioinformatics* 25, 3189–3190.
- Flower, B., Kennett, J., 1994. The middle Miocene climatic transition: East Antarctic ice sheet development, deep ocean circulation and global carbon cycling. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 108, 537–555.
- Folmer, O., Black, M., Hoeh, W., Lutz, R., Vrijenhoek, R., 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Mol. Mar. Biol. Biotechnol.* 3, 294–299.
- Fraser, C., Nikula, R., Spencer, H., Waters, J., 2009. Kelp genes reveal effects of subantarctic sea during the Last Glacial Maximum. *Proc. Natl. Acad. Sci. U. S. A.* 106, 3249–3253.
- Gersonde, R., Crosta, X., Abelmann, A., Armand, L., 2005. Sea-surface temperature and sea ice distribution of the Southern Ocean at the EPILOG Last Glacial Maximum—a circum-Antarctic view based on siliceous microfossil records. *Quat. Sci. Rev.* 24, 869–896.
- Gillespie, R., Baldwin, B., Waters, J., Fraser, C., Nikula, R., Roderick, G., 2012. Long-distance dispersal: a framework for hypothesis testing. *Trends Ecol. Evol.* 27, 47–56.
- González-Wevar, C.A., Nakano, T., Cañete, J., Poulin, E., 2010. Molecular phylogeny and historical biogeography of *Nacella* (Patellogastropoda: Nacellidae) in the Southern Ocean. *Mol. Phylogenet. Evol.* 56, 115–124.
- González-Wevar, C.A., Nakano, T., Cañete, J., Poulin, E., 2011a. Concerted genetic, morphological and ecological diversification in *Nacella* limpets in the Magellanic Province. *Mol. Ecol.* 20, 1936–1951.
- González-Wevar, C.A., David, B., Poulin, E., 2011b. Phylogeography and demographic inference in *Nacella (Patinigera) concinna* (Strebel, 1908) in the western Antarctic Peninsula. *Deep-Sea Res. II Top. Stud. Oceanogr.* 58, 220–229.
- González-Wevar, C.A., Díaz, A., Gérard, K., Cañete, J., Poulin, E., 2012a. Divergence time estimations and contrasting patterns of genetic diversity between Antarctic and southern South America benthic invertebrates. *Rev. Chil. Hist. Nat.* 85, 445–456.
- González-Wevar, C.A., Hüne, M., Cañete, J., Mansilla, A., Nakano, T., Poulin, E., 2012b. Towards a model of postglacial biogeography in shallow marine species along the Patagonian Province: lessons from the limpet *Nacella magellanica* (Gmelin, 1791). *BMC Evol. Biol.* 12, 139.
- González-Wevar, C.A., Chown, S., Morley, S., Coria, N., Saucède, T., Poulin, E., 2014. Out of Antarctica: recent colonization and speciation of the Antarctic limpet in sub-Antarctic Marion Island. *Polar Biol.* (submitted for publication).
- Griffiths, H., Barnes, D., Linse, K., 2009. Towards a generalized biogeography of the Southern Ocean benthos. *J. Biogeogr.* 36, 162–177.
- Griffiths, H., Arango, C., Munilla, T., McInnes, S., 2011. Biodiversity and biogeography of Southern Ocean pycnogonids. *Ecography* 34, 616–627.
- Gutt, J., Sirenko, B., Smirnov, I., Arntz, W., 2004. How many macrozoobenthic species might inhabit the Antarctic shelf? *Antarct. Sci.* 16, 11–16.
- Havermans, C., 2011. DNA barcoding reveals new insights into the diversity of Antarctic species of *Orchomene* sensu lato (Crustacea: Amphipoda: Lysianassoidea). *Deep-Sea Res. II Top. Stud. Oceanogr.* 58, 230–241.
- Haye, P.A., Varela, A.I., Thiel, M., 2012. Genetic signatures of rafting dispersal in algal-dwelling brooders *Limnoria* spp. (Isopoda) along the SE Pacific (Chile). *Mol. Ecol. Prog. Ser.* 44, 111–122.
- Heinrich, S., Zonneveld, K., Bickert, T., Willems, H., 2011. The Benguela upwelling related to the Miocene cooling events and the development of the Antarctic Circumpolar Current: evidence from calcareous dinoflagellate cysts. *Paleoceanography* 26, PA3209.
- Held, C., Wägele, J., 2005. Cryptic speciation in the giant Antarctic isopod *Glyptonotus antarcticus* (Isopoda: Valvifera: Chaetiliidae). *Sci. Mar.* 69, 175–181.
- Helmuth, B., Veit, R., Holberton, R., 1994. Long-distance dispersal of a subantarctic brooding bivalve (*Gaimardia trapesina*) by kelp-rafting. *Mar. Biol.* 120, 421–426.
- Ho, S., 2008. Evolutionary genetics—the molecular clock and estimating species divergence. *Nat. Educ.* 1, 1–2.
- Hüne, H., González-Wevar, C.A., Poulin, E., Mansilla, A., Fernández, D.A., Barrera-Oro, E., 2014. Dispersal vs. vicariance in the evolutionary history of Harpagifer fish species (Perciformes: Notothenioidei) from Antarctica and Patagonia/South America. *Polar Biol.* (submitted for publication).
- Hunter, R., Halanych, K., 2008. Evaluating connectivity in the brooding brittle star *Astrofoma agassizii* across the Drake Passage in the Southern Ocean. *J. Hered.* 99, 137–148.
- Jablonski, D., 1986. Larval ecology and macroevolution in marine invertebrates. *Bull. Mar. Sci.* 39, 565–587.
- Janosik, A., Mahon, A., Halanych, K., 2011. Evolutionary history of Southern Ocean *Odontaster* sea star species (Odontasteridae; Asteroidea). *Polar Biol.* 34, 575–586.
- Jokiel, P., 1990. Long-distance dispersal by rafting: reemergence of an old hypothesis. *Endeavour New Ser.* 14, 66–73.
- Kemp, A., Grigorov, I., Pearce, R., Naveira Garabato, A., 2010. Migration of the Antarctic Polar Front through the mid-Pleistocene transition: evidence and climatic implications. *Quat. Sci. Rev.* 29, 1993–2009.
- Knox, G.A., Lowry, J.K., 1977. A comparison between the benthos of the Southern Ocean and the North Polar Ocean with special reference to the Amphipoda and the Polychaeta. In: Dunbar, M.J. (Ed.), *Polar Oceans*. Arctic Institute of North America, Calgary, pp. 423–462.
- Krabbe, K., Leese, F., Mayer, C., Tollrian, R., Held, C., 2010. Cryptic mitochondrial lineages in the widespread pycnogonid *Colossendeis megalonyx* Hoek, 1881 from Antarctic and subantarctic waters. *Polar Biol.* 33, 281–292.
- Kumar, S., 2005. Molecular clocks: four decades of evolution. *Nat. Rev. Genet.* 6, 654–662.
- Lawver, L., Gahagan, L., Campbell, D., 2003. Evolution of seaways in the Circum-Antarctic region: implications for initiation of glaciation? *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 198, 11–37.
- Lear, C., Elderfield, H., Wilson, P., 2000. Cenozoic deep-sea temperatures and global ice volumes from Mg/Ca in benthic foraminiferal calcite. *Science* 287, 269–272.
- Lee, Y.-H., Song, M., Lee, S., Leon, R., Godoy, S.O., Cañete, I., 2004. Molecular phylogeny and divergence time estimations of the Antarctic sea urchin (*Sterechinus neumayeri*) in relation to the South American sea urchins. *Antarct. Sci.* 16, 29–36.
- Leese, F., Kop, A., Wägele, J., Held, C., 2008. Cryptic speciation in a benthic isopod from Patagonian and Falkland Island waters and the impact of glaciations on its population structure. *Front. Zool.* 5, 1–15.
- Leese, F., Agrawal, S., Held, C., 2010. Long-distance island hopping without dispersal stages: transportation across major zoogeographic barriers in a Southern Ocean isopod. *Naturwissenschaften* 97, 583–594.
- Lessios, H., Kessing, B., Robertson, D., Paulay, G., 1999. Phylogeography of the pantropical sea urchin *Euclidaris* in relation to land barriers and ocean currents. *Evolution* 53, 806–817.
- Lewis, A., Marchant, D., Ashworth, A., Hedenäs, L., Hemming, S., Johnson, J., Leng, M., Newton, A., Raine, J., Willenbring, J., Williams, M., Wolfem, A., 2008. Mid-Miocene cooling and the extinction of tundra in continental Antarctica. *Proc. Natl. Acad. Sci. U. S. A.* 105, 1–5.
- Linse, K., Griffiths, H., Barnes, D., Clarke, A., 2006. Biodiversity and biogeography of Antarctic and sub-Antarctic mollusca. *Deep-Sea Res. II Top. Stud. Oceanogr.* 53, 985–1008.
- Linse, K., Cope, T., Lörz, A., Sands, C., 2007. Is the Scotia Sea a centre of Antarctic marine diversification? Some evidence of cryptic speciation in the circum-Antarctic bivalve *Lissarca notorcadensis* (Arcoidea: Philobryidae). *Polar Biol.* 30, 1059–1068.
- Livermore, R., Nankivell, A., Eagles, G., Morris, P., 2005. Paleogene opening of Drake Passage. *Earth Planet. Sci. Lett.* 236, 459–470.
- Lomolino, M.V., Riddle, B.R., Brown, J.H., 2006. *Biogeography*, 3rd edition. Sinauer Associates, Inc., Sunderland, MA, (845 pp).
- Lyle, M., Gibbs, S., Moore, T., Rea, D., 2007. Late Oligocene initiation of the Antarctic Circumpolar Current: evidence from the South Pacific. *Geology* 35, 691–694.
- Macaya, E., Zuccarello, G., 2010a. DNA barcoding and genetic divergence in the giant kelp *Macrocystis* (Laminariales). *J. Phycol.* 46, 736–742.
- Macaya, E., Zuccarello, G., 2010b. Genetic structure of the giant kelp *Macrocystis pyrifera* along the southeastern Pacific. *Mar. Ecol. Prog. Ser.* 420, 103–112.
- Mackensen, A., 2004. Changing Southern Ocean palaeocirculation and effects on global climate. *Antarct. Sci.* 16, 369–386.
- Mahon, A., Thornhill, D., Norenburg, J., Halanych, K., 2009. DNA uncovers Antarctic nemertean biodiversity and exposes a decades-old cold case of asymmetric inventory. *Polar Biol.* 33, 193–202.
- Near, T., Dornburg, A., Kuhn, K., Eastman, J., Pennington, J., Patarnello, T., Zane, L., Fernández, D., Jones, C., 2012. Ancient climate change, antifreeze, and the evolutionary diversification of Antarctic fishes. *Proc. Natl. Acad. Sci. U. S. A.* 109, 3434–3439.
- Nikula, R., Fraser, C., Spencer, H., Waters, J., 2010. Circumpolar dispersal by rafting in two subantarctic kelp-dwelling crustaceans. *Mar. Ecol. Prog. Ser.* 405, 221–230. <http://dx.doi.org/10.3354/meps08523>.
- Orsi, A., Whitworth III, T., Nowlin Jr., W.D., 1995. On the meridional extent and fronts of the Antarctic Circumpolar Current. *Deep-Sea Res. I Oceanogr. Res. Pap.* 42, 641–673.
- Page, T., Linse, K., 2002. More evidence of speciation and dispersal across Antarctic Polar Front through molecular systematics of Southern Ocean *Limatula* (Bivalvia: Limidae). *Polar Biol.* 25, 818–826.
- Patarnello, T., Bargelloni, L., Varotto, V., Battaglia, B., 2007. Krill evolution and the Antarctic ocean currents: evidence of vicariant speciation as inferred by molecular data. *Mar. Biol.* 126, 603–608.

- Pearse, J., Mooi, R., Lockhart, S., Brandt, A., 2009. Brooders and species diversity in the Southern Ocean: selection for brooders or speciation within brooding clades? In: Krupnik, I., Lang, M.A., Miller, S. (Eds.), *Smithsonian at the Poles: Contributions to International Polar Year Science*. Smithsonian Institution Scholarly Press, pp. 181–196.
- Pfuhl, H., McCave, I., 2005. Evidence for late Oligocene establishment of the Antarctic Circumpolar Current. *Earth Planet. Sci. Lett.* 235, 715–728.
- Pierrat, B., Saucède, T., Brayard, A., David, B., 2013. Comparative biogeography of echinoids, bivalves and gastropods from the Southern Ocean. *J. Biogeogr.* 40, 1374–1385.
- Posada, D., Crandall, K., 2001. Intraspecific gene genealogies: trees grafting into networks. *Trends Ecol. Evol.* 16, 37–45.
- Raupach, M.J., Wägele, J.-W., 2006. Distinguishing cryptic species in Antarctic Assellota (Crustacea: Isopoda)—a preliminary study of mitochondrial DNA in *Acanthaspida drygalskii*. *Antarct. Sci.* 18, 191–198.
- Raupach, M., Malyutina, M., Brandt, A., Wägele, J., 2007. Molecular data reveal a highly diverse species flock within the munnopsoid deep-sea isopod *Betamorpha fusiformis* (Barnard, 1920) (Crustacea: Isopoda: Asellota) in the Southern Ocean. *Deep-Sea Res. II Top. Stud. Oceanogr.* 54, 1820–1830.
- Rintoul, S., Hughes, C., Olbers, D., 2001. The Antarctic circumpolar current system. In: Siedler, G., Church, J., Gould, J. (Eds.), *Ocean Circulation and Climate*. Academic Press, pp. 1–32.
- Rogers, A., 2007. Evolution and biodiversity of Antarctic organisms: a molecular perspective. *Philos. Trans. Biol. Sci.* 362, 2191–2214.
- Scher, H., Martin, E., 2006. Timing and climatic consequences of the opening of Drake Passage. *Science* 312, 428–430.
- Shaw, P., Arkhipkin, A., Al-Khairulla, H., 2004. Genetic structuring of Patagonian toothfish populations in the Southwest Atlantic Ocean: the effect of the Antarctic Polar Front and deep-water troughs as barriers to genetic exchange. *Mol. Ecol.* 13, 3293–3303.
- Shevenell, A., Kennett, J., Lea, D., 2004. Middle Miocene Southern Ocean cooling and Antarctic cryosphere expansion. *Science* 305, 1766–1770.
- Stankovich, A., Spalik, K., Kamler, E., Borsuk, P., Weglenski, P., 2002. Recent origin of sub-Antarctic notothenioids. *Polar Biol.* 25, 203–205.
- Strugnell, J.M., Allcock, A.L., 2013. Southern Ocean evolution in a global context: a molecular viewpoint. In: Verde, C., Di Prisco, G. (Eds.), *Adaptation and Evolution in Marine Environments Volume 01, The Impacts of Global Change on Environments*. Springer, Heidelberg New York Dordrecht London, pp. 35–53.
- Strugnell, J., Rogers, A., Prodöhl, P., Collins, M., Allcock, A., 2008. The thermohaline expressway: the Southern Ocean as a centre of origin for deep-sea octopuses. *Cladistics* 24, 853–860.
- Tavares, M., De Melo, G., 2004. Discovery of the first known benthic invasive species in the Southern Ocean: the North Atlantic spider crab *Hyas araneus* found in the Antarctic Peninsula. *Antarct. Sci.* 16, 129–131.
- Thatje, S., Fuentes, V., 2003. First record of anomuran and brachyuran larvae (Crustacea: Decapoda) from Antarctic waters. *Polar Biol.* 26, 279–282.
- Thatje, S., Hillenbrand, C., Larter, R., 2005. On the origin of Antarctic marine benthic community structure. *Trends Ecol. Evol.* 20, 534–540.
- Thompson, J., Higgins, D., Gibson, T., 1994. CLUSTALW: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. *Nucleic Acids Res.* 22, 4673–4680.
- Thornhill, D., Mahon, A., Norenburg, J., Halaných, K., 2008. Open-ocean barriers to dispersal: a test case with the Antarctic Polar Front and the ribbon worm *Parborlasia corrugatus* (Nemertea: Lineidae). *Mol. Ecol.* 17, 5104–5117.
- Thorpe, S., Heywood, K., Stevens, D., Brandon, M., 2004. Tracking passive drifters in a high resolution ocean model: implications for interannual variability of larval krill transport to South Georgia. *Deep-Sea Res. I Oceanogr. Res. Pap.* 51, 909–920.
- Verducci, M., Foresi, L., Scott, G., Sprovieri, M., Lirer, F., Pelosi, N., 2009. The Middle Miocene climatic transition in the Southern Ocean: evidence of paleoclimatic and hydrographic changes at Kerguelen plateau from planktonic foraminifers and stable isotopes. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 280, 371–386.
- Wares, J.P., Cunningham, C.W., 2001. Phylogeography and historical ecology of the North Atlantic. *Evolution* 55, 2455–2469.
- Waters, J., 2008. Driven by the West Wind Drift? A synthesis of southern temperate marine biogeography, with new directions for dispersalism. *J. Biogeogr.* 35, 417–427.
- Waters, J., Disjksra, L., Wallis, G., 2000. Biogeography of a southern hemisphere freshwater fish: how important is marine dispersal? *Mol. Ecol.* 9, 1–7.
- Wilson, N., Hunter, R., Lockhart, S., Halaných, K., 2007. Multiple lineages and absence of panmixia in the “circumpolar” crinoid *Promachocrinus kerguelensis* from the Atlantic sector of Antarctica. *Mar. Biol.* 152, 895–904.
- Wilson, N., Schrödl, M., Halaných, K., 2009. Ocean barriers and glaciation: evidence for explosive radiation of mitochondrial lineages in the Antarctic sea slug *Doris kerguelensis* (Mollusca, Nudibranchia). *Mol. Ecol.* 18, 965–984.
- Xia, X., Xie, Z., 2001. DAMBE: software package for data analysis in molecular biology and evolution. *J. Hered.* 92, 371–373.
- Zachos, J., Pagani, M., Sloan, L., Thomas, E., Billups, K., 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* 292, 686–693.