



SYMPOSIUM

Effects of Capability for Dispersal on the Evolution of Diversity in Antarctic Benthos

Sven Thatje¹

Ocean and Earth Science, University of Southampton, National Oceanography Centre, Southampton, European Way, SO14 3ZH, Southampton, UK

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¹E-mail: svth@noc.soton.ac.uk

Synopsis The likelihood of marine invertebrates to maintain large geographic ranges is widely dependent on the ability of their early ontogenetic stages to disperse over long distances. Marine benthic invertebrates inhabiting the cold-stenothermal environment of the Southern Ocean are known for their overall reduced number of pelagic larvae, or drifting stages of any kind, when compared with organisms elsewhere in the sea. The diversity of organisms thriving in Antarctic waters is the result of evolution *in situ* and of the intrusion of species from surrounding seas. The reasons for a high level of endemism and a stunning diversity of benthic invertebrates found today are frequently discussed in the literature, but the mechanisms whereby diversity has been controlled over time remain largely theoretical. Here, I suggest that, indeed, early life-history patterns play a key role in defining the radiation and the speciation potential of Antarctic benthic invertebrates. In arguing this case, I synthesize the growing body of molecular studies on population connectivity in Antarctic benthic invertebrates, and compare this information with knowledge of their life histories and biogeography. I conclude that differences in early life-history patterns are key to the resilience potential of species in response to late Cenozoic glacial periods and propose that there is a direct relationship between rate of speciation and the ability of taxa to disperse.

Introduction

Historically, one of the most controversial concepts in marine ecology has been the question of a latitudinal gradient in the occurrence of pelagic planktonic larvae (Thorson 1936, 1950; Mileikovsky 1971; Clarke 1992; Arntz and Gili 2001; Thatje et al. 2003, and references therein). Based on his pioneering work carried out in Danish and Arctic waters, Danish benthologist Gunnar Thorson suggested that the decline in the occurrence of pelagic larval forms with increasing latitude is an adaptation to the mismatch of prolonged developmental times and short seasons of food availability, ultimately selecting against the occurrence of a feeding stage in pelagic larvae in polar seas. What later became known as Thorson’s rule, named by Mileikovsky (1971), has for decades, dominated the discussions of whether reproductive patterns in polar

invertebrates are really any different from elsewhere in the sea. Unsurprisingly, and in particular for the Antarctic marine realm, any records of pelagic larvae in polar seas have subsequently been used to challenge Thorson’s concept (for discussion see: Clarke 1992; Pearse et al. 1994; Poulin and Feral 1996; Stanwell-Smith et al. 1997; Gallardo and Penchaszadeh 2001, Thatje et al. 2005d, and references therein).

There is no doubt that since Thorson’s early works, the field of invertebrate reproduction has seen a tremendous progress in our understanding of the ecology and physiology that underlie invertebrate reproductive traits. For instance, Thorson distinguished between planktonic (pelagic) and lecithotrophic (benthic) larvae (Mileikovsky 1971). Today, we know of a great variety of intermediate larval feeding modes both in benthic and pelagic

larvae (e.g., Anger 2001; Anger et al. 2002, and references therein). The total number of described larval morphotypes known from the Southern Ocean is still less than 250 (Stanwell-Smith et al. 1997, 1999; Thatje et al. 2005d), which stands in great contrast to an estimated more than 15,000 species of benthic invertebrates (with about 8200 species scientifically described so far) (see Griffiths 2010; Clarke and Johnston 2003) potentially inhabiting the continental shelves of Antarctica (Gutt et al. 2004). The most important work of recent years is undoubtedly that of Stanwell-Smith et al. (1997, 1999) describing 131 larval types for waters off Signy Island. This record may even be an underestimation of species found there since the identification of larvae is difficult without standardized taxonomic local keys or the use of molecular tools. Nevertheless, it does not change the fact that despite decades of research since Thorson provided us with his groundbreaking insights, the low diversity, as well as low abundance, of planktonic larval forms in Antarctic waters remains apparent.

In this synthesis I elaborate on the idea that the early life cycle, and in particular, the ability of early ontogenetic stages to disperse, plays a key role in the evolutionary history of Antarctic benthic invertebrates. Although this may be intuitive to marine ecologists, the link between the degree of complex early life history, distribution range, and species diversity, is less obvious in Antarctica. The question of pelagic versus non-pelagic larvae remains of significance in this context, but I will argue herein that it is the peculiarities of ecological and physiological adaptations in Antarctic benthic invertebrates and the effects of those attributes on reproductive modes that are key to their resilience over time, and in particular, in response to late Cenozoic glacial–interglacial cycles (Crame 1999; Thatje et al. 2005d, 2008).

Although I personally regard Thorson's macroecological concept to be conclusive, there are ecological and physiological parameters prevailing in cold waters that may have led to an underestimation of the number of existing larval forms and the diversity in nutritional states, and that combine to directly affect the potential ability of a species to disperse; (1) longevity in Antarctic invertebrates may contribute to an underestimation of the total number of pelagic larval forms and of the frequency of successful recruitment (Dayton and Oliver 1977; Dayton 1989); (2) as a consequence of longevity, reproduction may be more irregular and successful recruitment via pelagic life stages may be sporadic and even less frequent, for example, occurring less than once in a decade (Dayton and Oliver 1977; Dayton

1989); (3) reproductive effort might be directed to periods with more favorable conditions for larvae even within a narrow temperature window (Stanwell-Smith and Peck 1998); (4) prolonged developmental times, as a result of low polar temperatures, may aid dispersal in any form of early life-history stage regardless of whether the larvae are pelagic or benthic; the pelagic larval stage may be short and inappropriate for use as a general indicator of long-distance dispersal (cf. Wilson et al. 2007); (5) simple comparisons of egg sizes as an energetic measure across latitudes may not always be a valid measure of energy contents, as so often is used as an indirect measure of lecithotrophy (Anger et al. 2002; Thatje and Mestre 2010; Hall and Thatje 2012); and (6) the means of transport of early life-history stages are more diverse than previously believed.

Today, we distinguish a range of nutritional states associated with both pelagic and benthic (demersal) larvae. Lecithotrophy (endotrophy) in development occurs in benthic brooders, as well as in broadcasters with pelagic larvae, and many intermediate forms of feeding ranging from facultative lecithotrophy to full planktotrophy, can be found in marine invertebrates. However, we know very little about these modes in polar invertebrates and what we do know is usually concentrated in specific taxonomic groups, thanks to dedicated careers of individual scientists. This, together with the limited available knowledge of invertebrate reproduction in the cold, however, may bias the scientific community's perception of macroecological patterns.

Knowledge of reproductive modes is important for an understanding of the evolution of the diversity of organisms in the Antarctic benthos. I will argue this case by discussing examples of species with known geographic ranges, and for which we have knowledge of genetic population identity, thanks to the increasing body of data from molecular biological works in recent years (Grant et al. 2011). I believe that the combination of the emergent molecular tools and traditional approaches to larval developmental biology will be a key to increasing our understanding of the evolution of life in cold waters.

Antarctic evolution in a nutshell

Antarctica is the most isolated continent on earth, isolated physically by a strong Antarctic Circumpolar Current (ACC), the polar frontal system, a circum-Antarctic deep ocean, and physiologically by low, and often sub-zero, temperatures (Fig. 1). Life in Antarctica as seen today is the result of the geotectonic history of the continent and the associated

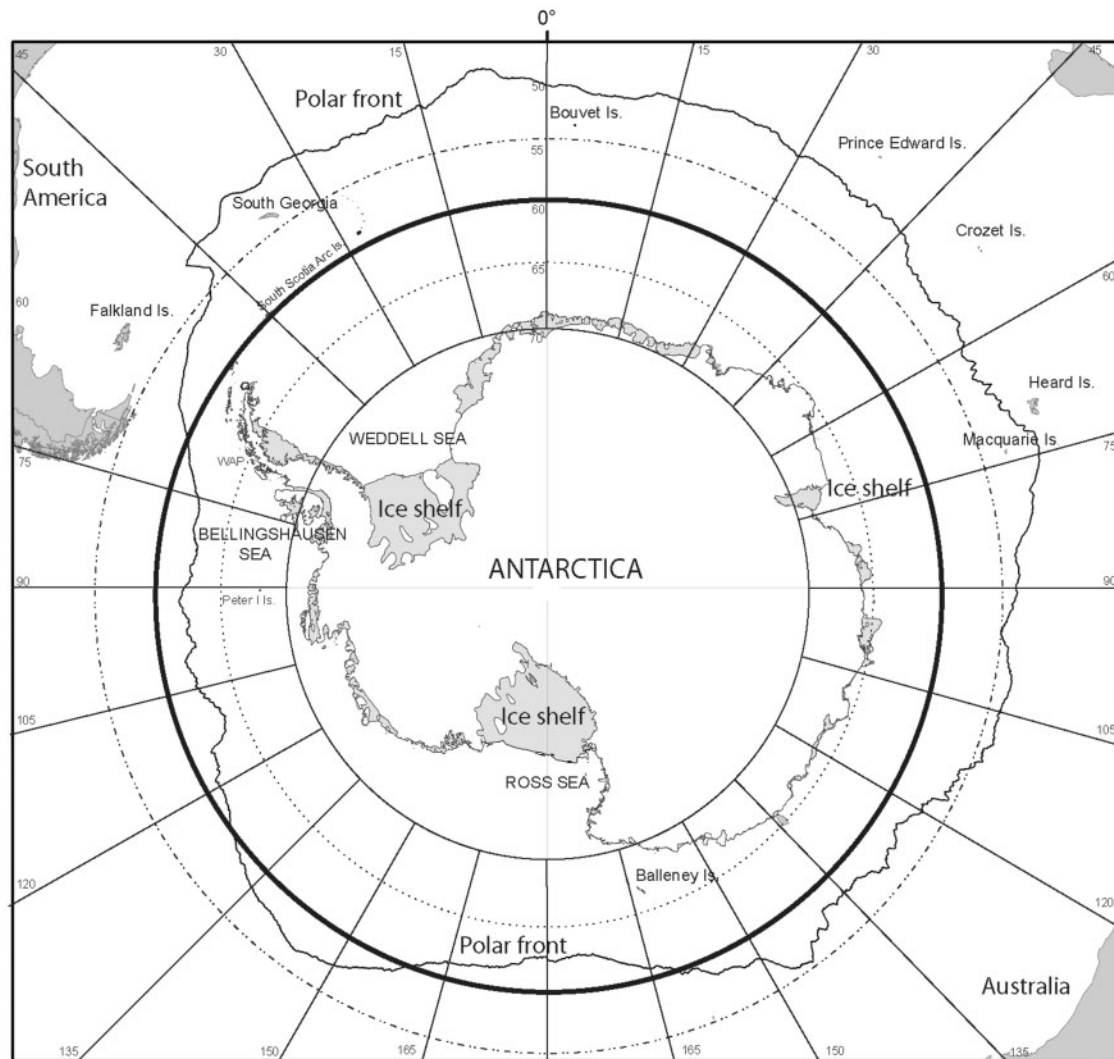


Fig. 1 Schematic of the Southern Ocean and Antarctica, with focus on oceanographic and geological features.

climatic change dating back as far as the breakup of the Gondwana supercontinent in the early Jurassic, about 200 Ma ago. However, it is not until the late Cretaceous, about 70 Ma that the Antarctic continent, still connected through shallow-water gateways with Australia and South America, somehow resembled the overall shape of the continent as seen today (Lawyer et al. 1992; Crame 1999).

There is general consensus that the onset of southern hemispheric cooling, starting at the Paleocene–Eocene boundary, about 55 Ma, defined the climatic evolution of the Southern Ocean (Crame 1999, and references therein). This process, often referred to as Antarctic cooling, followed several cooling steps, with the last one not occurring until about 14 Ma ago (Zachos et al. 2001; Shevenell et al. 2004). Significant in this process was the opening of ocean gateways around Antarctica, in particular, the Drake

Passage at about 30 Ma ago (Lawyer et al. 1992). This allowed for the formation of the vigorous and deep-reaching ACC, which is the main force behind the physical and physiological (thermal) isolation of the Southern Ocean, with the Polar Front being its most enigmatic oceanographic feature (Fig. 1). The exact timing of the opening of Drake Passage is controversial and varies from 6 to 41 Ma ago (Scher and Martin 2004; Lyle et al. 2007). In addition, it remains unclear whether the onset of the ACC was responsible for the overall cooling of the Southern Ocean and glaciation of East Antarctica, or whether glaciation alone drove overall cooling.

Molecular biology may provide some answers to this problem in dating; whereas Chen et al. (1997) put the radiation of the Antarctic teleost icefish (Notothenioidae) at about 15 Ma (but see Bargelloni et al. 2000), the radiation of brooding

peracarid amphipods of the Antarctic species of the family Epimeridae was estimated at 15.7 Ma (Lörz and Held 2004). However, the fossil record in support of change in the benthic community over geological time is very limited because of the permanent ice cover of Antarctica. The only fossil data supporting prehistoric dispersal are those of Beu et al. (1997) which suggest that radiation events in bivalve molluscs occurred at the Oligocene–Early Miocene and Miocene–Pliocene boundaries, thereby supporting circum-Antarctic dispersal/radiation.

Today's benthic communities inhabiting the Antarctic continental shelf are not only unique in species richness, but also in community structure. Particularly striking is the absence of benthic predators that structure benthic communities elsewhere in shallow seas: durophagous bony fish, sharks, crabs, and rays are absent or rare. The absence of durophagous predators has been reported throughout the limited fossil record of Antarctica and has been linked to an inability to rise to the physiological challenges of adaptation to cold (see Aronson et al. 2007; Peck 2002; Thatje et al. 2005b, and references therein). The stunning diversity and flourishing of other groups such as peracarid crustaceans and a high diversity of benthic filter feeders may be directly or indirectly linked to reduced pressure from predation (Aronson et al. 2007).

The Antarctic fauna has a long history of evolution *in situ* (Dell 1972; Clarke and Crame 1989, 2010). Phylogenetic studies (Brandt 1991, 1992) indicate that some groups' evolutionary past dates back further than the onset of Antarctic cooling, and strong biogeographic affinities are evident between Antarctica and the Magellanic sub-Antarctic region (Arntz et al. 2005). Nevertheless, a high degree of endemism in the Southern Ocean points at a long period of isolation (Clarke and Crame 2010). Phylogeographic work in recent years indicates that evolution *in situ*, as well as faunal exchange with surrounding seas, may have been significant over a long time, and speciation across the oceanographic frontal system of the Polar Front, as well as deep-sea radiation of species in and out of the Southern Ocean, is possible (Page and Linse 2002; Brandt et al. 2007; Wilson et al. 2009; Krabbe et al. 2009).

A striking feature of the more recent climatic history is the advance and retreat of the Antarctic continental ice cap in glacial–interglacial cycles, known as Milankovitch cycles. During the late Cenozoic, approximately the last 2.5 Ma, the advance of the grounded ice sheet across the continental shelf to the outer shelf break erased the benthos around Antarctica. A modeling approach suggests that the

continental shelf may have been completely covered by grounded ice sheets at least at maximum glacial extent, which would have left little, or no refuge for the benthos (Huybrechts 2002). However, the extent of ice certainly followed diachronous—time transgressive—fluctuations, and either persistent shelters or migration from one shelter to another may have allowed benthos to dodge extinction (Thatje et al. 2005d, 2008). At the shelf's edge, the grounded ice masses released huge amounts of glaciogenic debris, which was then redeposited down the continental slope by sedimentary gravity flows, such as slides, debris, and turbidity flows. Overall, glacial periods exposed the shelf's benthos to large-scale disturbances that greatly exceeded the levels of disturbance by grounded ice seen today (Gutt and Piepenburg 2003; Thatje et al. 2005d, 2008). Further, the binding of water in land-based glaciers and ice sheets caused drastic and rapid changes in sea level during those times, likely influencing ocean currents in the Southern Ocean (Lambeck and Chappell 2001; Lambeck et al. 2002; Edwards 2006).

It is argued that the genetic diversity of populations found today, especially in shallow-water benthic taxa with strong depth zonation by depth, is mainly a reflection of habitat availability during that period (for discussion, see Thatje et al. 2005d). Although in many cases the evolutionary history of shallow Antarctic benthos likely dates back to earlier periods, the rather extreme changes in habitat, and possibly in availability of food (Thatje et al. 2008) may have been the predominant selective forces shaping the genetic identity of today's shelf species. In this context, Pearse et al. (2009) emphasize however, that brooding is likely an evolutionary adaptation dating back to periods prior to Antarctic cooling and that its predominance in many Antarctic invertebrate taxa is unlikely a specific adaptation to polar conditions. Conversely, environmental conditions prevailing in the Last Glacial Maximum (LGM) may have widely selected against pelagic larvae that rely upon primary productivity (for discussion, see also Thatje et al. 2008).

The ability of extant species to survive glacials may have been directly related to their ability to respond to changing conditions, for instance by either surviving in small populations in shelf refugia and/or the ability to seek refuge elsewhere in the deep Southern Ocean, such as in the deep sea adjacent to the shelf (Brey et al. 1996; Raupach et al. 2009), or even in the sub-Antarctic. Indeed, the ability to disperse or migrate over long distances must have been a key element in survival during those periods.

Dispersal mechanisms in Antarctic invertebrates

A whole range of dispersal mechanisms of Antarctic marine invertebrates are known, many of which are typical of benthic invertebrates elsewhere in the sea. Differences in dispersal times as a result of slow development in the cold, however, can result in exceptional distributional ranges, such as the circum-Antarctic distributional pattern of invertebrates (Dell 1972; Pearse et al. 1991; Clarke and Johnston 2003), a concept that has traditionally been based on the identification of constant morphological characters among populations of the same species. Here, an overview of dispersal mechanisms follows, highlighting a range of Antarctic-specific means of transport.

Pelagic dispersal modes

Pelagic drift of any kind is still considered the most effective dispersal mechanism. Invertebrates with partial or full pelagic larval development have an opportunistic advantage in early colonization of new habitats, such as those resulting from local ice scour. Despite being found in low numbers, larvae of certain taxa seem to occur year-round or over several seasons. Although containing a high number of brooders as well, echinoids and ophiuroids are found as planktotrophic larvae (Pearse et al. 1994; Poulin and Feral 1996; Stanwell-Smith et al. 1999). Of the bivalve species of the continental shelf in the Weddell Sea, studied by Hain and Arnaud (1992), 14 out of 44 species appeared to have planktotrophic larvae, but the absence of any bivalve larvae from the plankton suggests that any bivalve offspring might be of demersal occurrence or of short duration. A classical example of a fully planktotrophic development is that of the three most abundant continental shelf/slope caridean shrimp species *Chorismus antarcticus*, *Notocrangon antarcticus*, and *Nematocarcinus lanceopes* (Bruns 1992; Thatje et al. 2005c, 2005a) and it is likely that Southern Ocean shrimp species follow this pattern. The majority of filter and suspension feeders, such as ascidians, sponges, and bryozoans are generally known to follow a short-lived pelagic life cycle, often lecithotrophic, although few case studies have clearly proven this for Antarctic representatives (e.g., Brito et al. 1997).

Benthic dispersal modes

The ability of larvae and juveniles to distribute by means of demersal living and by benthic currents has generally been neglected. Several studies suggested that absence from the water column should indicate

larvae to be benthic living (e.g., Hain and Arnaud 1992; Thatje and Mestre 2010), but systematic sampling of bottom waters for larvae and early juveniles has only rarely been attempted. Given the slow developmental rates and potentially long drift times in Antarctic invertebrate larvae, however, demersal drift over long periods may be an important transport mechanism, comparable with pelagic transport. Significant in this context is the effect of ice scour by grounded ice masses, typical of Antarctic shelves all around the continent, resuspending benthic material and organisms. Ice scour may aid the dispersal of fragmented colonial benthos, such as bryozoans, hydrozoans, and sponges, which may be able to re-establish elsewhere; this is an often-disputed assumption that still demands experimental proof. Even more important in this process may be the mobilization of epifauna attached to such fragmented organisms, which may carry such animals as bivalves or even peracarid crustaceans over otherwise impossible distances (Helmuth et al. 1994; Higgs et al. 2009). Benthic dispersal should be the predominant possibility of transport for brooding species, many echinoderms, bivalves, polychaetes, and the extremely diverse peracarids, but achievable dispersal distance might be limited overall (see next chapter). Rather peculiar means of transport have been reported for benthic bivalves, which successfully passed through the gut of the notothenioid fish, *Notothenia coriiceps* (Domaneschi et al. 2002). It is therefore likely that future autecological studies will yield further means of transport for benthic invertebrates and their offspring.

Rafting

In an environment in which the Westwind Drift is driving the ACC as the predominant current system clockwise around the Antarctic continent, rafting on macroalgae and debris of any kind might be a successful way to disperse over long distances (Dell 1972; Barnes 2002), and was tested by Highsmith (1985) and observed by Helmuth et al. (1994) for the brooding pelecypod bivalve *Gaimardia trapesina*. Though the ACC is the most prominent current in the Southern Ocean, the counter-clock current closer to the continent, as well as more regional gyre systems of significance, such as the Weddell Sea Gyre, may significantly aid dispersal of invertebrates by means of rafting (Barnes 2002; Arntz et al. 2005). The potential for successful expansion of the geographic range and establishment of new populations by rafting may be high for brooders, as a new area

could be colonized by just a single brooding female (Pearse and Lockhart 2004; Higgs et al. 2009).

It has long been recognized that pumice and driftwood can move both into and out of the Southern Ocean (Barber et al. 1959; Coombs and Landis 1996). Such means of transport might be recurrent in areas of tectonic spreading zones, such as the Scotia Arc, although occurrence of pumice might be extremely irregular and evidence for associated rafting fauna is rare and to date has only been found in two kelp-associated peracarid crustaceans (but see Nikula et al. 2010).

Anthropogenic means of transport

It is noteworthy that human activities may increasingly support the introduction of marine organisms into Antarctica. Warming of the climate is lowering the physiological barrier of low temperature to invasion, in particular, along the rapidly warming waters off the Western Antarctic Peninsula (Meredith and King 2005), and may open up niches for the establishment of invasive species with unprecedented consequences for the native fauna (Aronson et al. 2007). In this context, the transport of sub-Antarctic and already rather cold-adapted species by means of fouling on ship hulls (Lee and Chown 2009), or by transport in ballast water should be recognized (Aronson et al. 2011).

The direction of larval transport is driven by local and large-scale current systems, of which the ACC is the most prominent one in the Southern Ocean (Fig. 1). Local retention in gyre systems even at larger scales (e.g., Weddell Sea Gyre) is possible and may enhance the distribution of cryptic species and the gene flow among populations. More recently, it has become evident that eddy systems might be a means of crossing oceanographic frontiers as strong as the Polar Front, thereby providing means of transport for larvae from otherwise physically isolated regions, such as the northern and southern branches of the Scotia Sea (Thatje and Fuentes 2003; Arntz et al. 2005; Glorioso et al. 2005). Strengths of ocean currents in the Southern Ocean may have been different or changed in direction during glacial periods (Lambeck and Chappell 2001; Lambeck et al. 2002) as a result of the extent of continental ice extent and of permanent cover by sea ice in vast areas of the Southern Ocean (Thatje et al. 2008) and may have affected dispersal by the drifting of early ontogenetic of any kind in different ways than seen today (cf. Page and Linse 2002). This area of research requires much more future attention

and collaboration of biologists, (paleo)-oceanographers, and modelers.

Effects of dispersal modes on (genetic) diversity

The use of genetic studies to assess the genetic variability of Antarctic organisms has given rise to a new era of understanding species delineation, cryptic species (species representing a high level of genetic difference but which resemble one another morphologically), and population (haplotype) diversity that may indicate the level of genetic connectivity among populations (e.g., Page and Linse 2002; Janosik et al. 2011; Hoffman et al. 2012). Further, the use of DNA sequences offers novel opportunities to identify marine invertebrate larvae and helps understand better life-history patterns in benthic invertebrates (Webb et al. 2006; Janosik et al. 2008; Heimeier et al. 2010; Mahon et al. 2010). Of all marine taxa that have been studied by molecular means to date, the arthropods and, in particular, the Peracaridea have received most attention (Grant et al. 2011).

Although a relatively young area of research in an Antarctic context, a few years of study have identified an unexpected number of cryptic species in Antarctica, mostly from the continental shelves. Cryptic speciation seems particularly common in the brooding peracarid crustaceans, which are most species-rich in the Southern Ocean (Clarke and Johnston 2003), and have been found not only on the continental shelves but also in the adjacent deep sea (Held 2003; Raupach et al. 2007, 2009). Cryptic species have also been reported in echinoderms such as ophiuroids, echinoids, and brooding pycnogonids (Table 1 for more examples; Fig. 2).

Unsurprisingly, the growing body of work on cryptic speciation has been used to challenge the traditional concept that many Antarctic benthic invertebrates have a circum-Antarctic distribution (Dell 1972). In support of this, various shallow-water taxa have also been split into new species or species-clusters following genetic study (e.g., Lörz et al. 2009; Brandão et al. 2010), but has the circum-Antarctic species concept really lost its validity? The study by Raupach et al. (2010) clearly demonstrated that there is a direct relationship between larval dispersal mode and circum-Antarctic distribution. In their study of the shallow-water shrimp *C. antarcticus* and the deep-sea shrimp *N. lanceopes*, the authors evidenced by the use of two mitochondrial and one nuclear gene fragment that regional genetic differentiation was apparent without cryptic speciation, supporting the circum-Antarctic species

Table 1 Cases of genetic diversity in Antarctic benthic invertebrates. Comparison with species distributional ranges provides an indirect measures of potential for dispersal

Species	Genetic pattern	Study area	Reproductive mode	Genetic marker	Reference
<i>Chorismus antarcticus</i> (Decapoda)	Panmixia, reduced haplotype diversity, post-glacial expansion	Circum-Antarctic (shelf depth)	Planktotrophic larva	COI, 16S 18S, 28S	Raupach et al. 2010, Thatje et al. 2005a
<i>Nematocarcinus lanceopes</i> (Decapoda)	Panmixia, high haplotype diversity	Circum-Antarctic (deep sea and deep continental slope)	Planktotrophic larva	COI, 16S 18S, 28S	Raupach et al. 2010, Thatje et al. 2005a
<i>Lissarca notorcadensis</i> (Bivalvia)	Cryptic speciation	Sub-Antarctic, weddell Sea, WAP, Ross Sea	Brooder	COI	Linse et al. 2007
<i>Margarella Antarctica</i> (Bivalvia)	Highly restricted gene flow	WAP	Brooder	AFLP	Hoffman et al. 2011a
<i>Nacella concinna</i> (Gastropoda)	Homogenous species, differentiation at population level	Scotia sea islands, WAP	Planktotrophic larva	COI, AFLPs	Gonzalez-Wevar et al. 2011; Hoffman et al. 2011a, 2011b
<i>Doris kerguelenensis</i> (Nudibranchia)	Rapid post-glacial expansion; potentially cryptic species	Circum-Antarctic	Direct developer	COI	Wilson et al. 2009
<i>Promachocrinus kerguelensis</i> (Crinoidea)	Some haplotype diversity found; intermediate, suggesting limited pelagic dispersal	WAP and Scotia sea	Short pelagic larva (?)	COI, CytB	Wilson et al. 2007
<i>Promachocrinus kerguelensis</i> (Crinoidea)	Circum-Antarctic; sympatric in seven mitochondrial lineages, restricted gene flow, East Antarctica	Circum-Antarctic	Short pelagic larva (?)	COI, CytB, 16S, 28S, ITS	Hemery et al. 2012
<i>Astrotoma agassizii</i> (Ophiuroidea)	Homogenous population at intermediate scale (>500 km)	Drake Passage	Brooder, some dispersal potential shown	COII, 16S rRNA	Hunter and Halanych 2008
<i>Astrotoma agassizii</i> (Ophiuroidea)	Evidence for likely cryptic speciation in South America; homogenous populations in Ross Sea	Ross Sea	Possibly planktonic larva in Antarctica, brooding in South American lineages (?)	COI, 16S	Hunter and Halanych 2008, Heimeier et al. 2010
<i>Ophionotus victoriae</i> (Ophiuroidea)	Evidence for cryptic speciation; some genetically homogenous populations	WAP, Southern Ocean Islands	Planktotrophic larva (short duration?)	COI, 16S	Hunter and Halanych 2010
<i>Odontaster</i> species (Astyeroidea)	Multiple species found, cross ACC distribution in <i>O. meridionalis</i> , restricted distribution to either side of Polar Front in other <i>Odontaster</i> species.	WAP, sub-Antarctic/ Atlantic, Ross Sea	Pelagic larva	COI, 16S	Janosik et al. 2011
<i>Abatus cordatus</i> (Echinoidea)	Significant differentiation at the population level	Kerguelen Islands (endemic)	Brooder	Microsats, EPIC markers	Ledoux et al. 2012
<i>Parbolasia corrugatus</i> (Nemertea)	Cryptic speciation (but low diversity; two forms)	South Orkney Islands; sub-Antarctic and circum-Antarctic	Planktotrophic larva	COI	Rogers et al. 1998; Thornhill et al. 2008
<i>Eusirus perdentatus</i> , <i>Eusirus giganteus</i> (Amphipoda)	Highly restricted gene flow, possible cryptic speciation and/or speciation	Circum-Antarctic	Brooder	COI, CytB, ITS2	Baird et al. 2011
<i>Durvillaea antarctica</i> (Amphipoda)	Single haplotype found	Circum-Antarctic through rafting on kelp	Brooder	COI	Nikula et al. 2010

(continued)

Table 1 Continued

Species	Genetic pattern	Study area	Reproductive mode	Genetic marker	Reference
<i>Orchomenella franklini</i> (Amphipoda)	High genetic differentiation	East Antarctica	Brooder	Microsats	Baird et al. 2012
<i>Leucon</i> species-complex (Cumacea)	Potentially cryptic species, although more evidence needed	WAP, Weddell and Ross seas, circum-Antarctic	Brooder	COI, 16S	Rehm 2009
<i>Acanthaspidia drygalskii</i> (Isopoda)	Some evidence for cryptic speciation	Circum-Antarctic, also deep sea	Brooder	16S	Raupach and Wägele 2006
<i>Betamorpha fusiformis</i> (Isopoda)	Cryptic speciation	Deep sea	Brooder	16S, 18S	Raupach et al. 2007
<i>Septemserolis septemcarinata</i> (Isopoda)	Significant genetic differentiation found, but one species still; result of recent expansion or rafting?	Scotia sea to Bouvet	Brooder	COI, Microsats.	Leese et al. 2010
<i>Glyptonotus antarcticus</i> (Isopoda)	Cryptic speciation	Circum-Antarctic	Brooder	16S	Held and Wägele 2005
<i>Ceratoserolis trilobitoides</i> (Isopoda)	Cryptic speciation	Circum-Antarctic	Brooder	16S Microsat.	Held 2003, Leese and Held 2008
<i>Limnoria stephenseni</i> (Isopoda)	Single haplotype found	Circum-Antarctic through rafting on kelp	Brooder	COI	Nikula et al. 2010
<i>Macrosclapha tensa</i> (Ostracoda)	Increased number of cryptic and morpho-species	Circum-Antarctic (Weddell Sea, Ross Sea)	Brooder	COI, ITS	Brandão et al. 2010
<i>Nymphon australe</i> (Pycnogonida)	Cryptic speciation	Circum-Antarctic	Brooder	COI, 16S	Mahon et al. 2008; Arango et al. 2010
<i>Colossendeis megalonyx</i> (Pycnogonida)	Cryptic speciation	Antarctic and sub-Antarctic	Brooder	COI	Krabbe et al. 2009

concept. This is significant because both species have planktotrophic larvae that persist in the water column for several months, thereby aiding long-distance dispersal (Thatje et al. 2005c, 2005a). Furthermore, the study indicated a Pleistocene population expansion in *C. antarcticus*, suggesting a demographic, post-glacial expansion following habitat contraction during glaciation of the continental shelf. In contrast, the deep sea, which is habitat for *N. lanceopes*, allowed this species to develop and most importantly, maintain higher haplotype diversity, whereas glacial periods led to an impoverished diversity in the shallow-water shrimp. The potential advantage of broadcasters over brooders to maintaining large distribution areas is possible best supported by the study of Hoffman et al. (2011) in which the authors present a more restricted gene flow in the brooding molluscs *Margarella antarctica* compared with the broadcasting *Nacella concinna* along the Antarctic Peninsula.

Such evidence supports the direct advantage of broadcasters versus brooders in maintaining genetically homogeneous populations and species-identity

over long geographic distances. This is also and indirectly supported by the cryptic speciation and high population diversity found in Southern Ocean deep-sea peracarids (Table 1). It should however, be noted that sampling effort and advance of molecular approaches over time may complicate generalizations. In an early work on genetic diversity of the crinoid *Promachocrinus kerguelensis* sampled along the West Antarctic Peninsula (WAP, Fig. 1), Wilson et al. (2007) supported the view that the short occurrence of pelagic drifting stages assumed for this species increases genetic distance among populations over intermediate distance. In contrast, more recent study by Hemery et al. (2012), using large dataset from around Antarctica, demonstrated high connectivity between populations over wide areas of the Southern Ocean and in particular, along the Antarctic Peninsula. This example quite strikingly demonstrates how our view of genetic diversity pattern may change in individual taxa as molecular approaches develop and large-scale sampling has been achieved. Nevertheless, this may not entirely contradict previous work, because barriers to gene

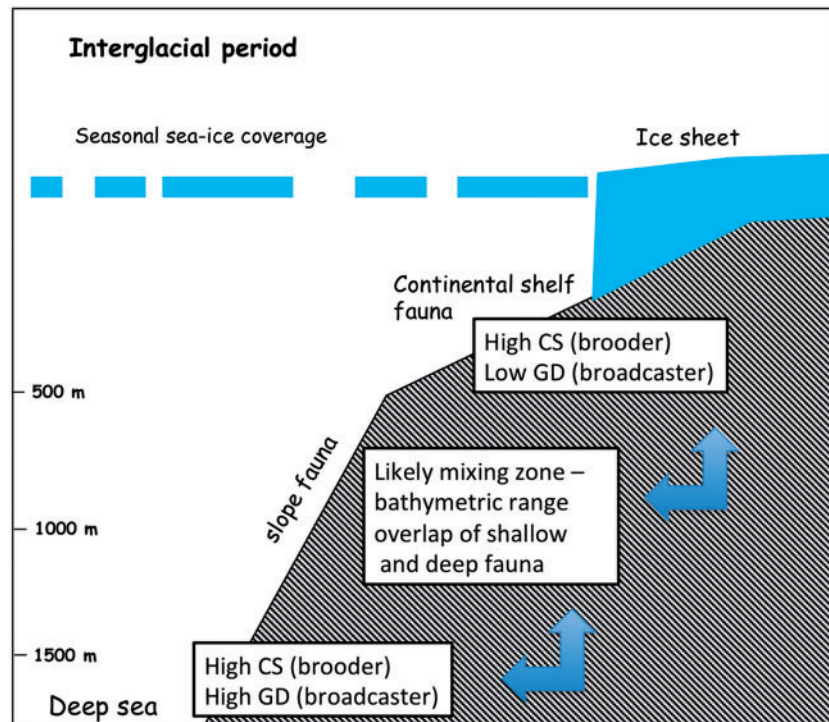


Fig. 2 Schematic of genetic diversity found in shallow and deep waters off Antarctica, as interpreted from available case studies; Overall, low genetic diversity in broadcasters and high level of cryptic speciation is suggested for invertebrates inhabiting the Antarctic continental shelf. In contrast, broadcasters maintain high genetic diversity in the circum-Antarctic deep sea; the continental slope is likely a mixing zone of deep- and shallow-water characteristics in genetic pattern, with deep fauna emerging onto the slope (cf. Brey et al. 1996; Thatje et al. 2005d); exceptions from this overall suggested pattern for individual taxa are likely. CS, cryptic speciation; GD, Genetic diversity (population level; cf. Table 1).

flow appeared evident in East Antarctica and given the uncertainty about its larval developmental mode and developmental time in the pelagic, *P. kerguelensis* may not contradict the hypothesis developed in this article. The example does furthermore imply that, indeed, local conditions, for example, in current intensity may foster or restrict the gene flow independent of developmental mode, which may potentially explain restricted gene flow in East Antarctica in comparison with the Antarctic Peninsula region (for details, see Hemery et al. 2012). Finally, it should be highlighted however, that two brooding peracarid species were found to maintain panmixia by means of rafting on macroalgae (Nikula et al. 2010) and therefore, achieving circum-Antarctic distribution is not exclusive to broadcasters alone.

The question arises: do broadcasters really have an evolutionary advantage over brooders in Antarctic waters? Brooders limited to shallow waters may have marginally dodged extinction during glacial periods, but nevertheless, seem to dominate the Antarctic benthos in terms of species richness. This holds particularly true for the peracarid amphipods and isopods, and may be similar for other groups

that scarcely have been studied so far (but for discussion of brooding in echinoderms, see Poulin and Feral 1996). If evolutionary success is measured by the ability of a single species to maintain its distributional area over long periods of time, then the example of the Antarctic shrimp may be the answer. If we measure evolutionary success as the ability of a taxonomic group to respond to an evolutionary bottleneck by developing even more sophisticated ecotypes resulting in increased diversity, then the peracarid crustaceans must be considered champions of Antarctic diversity.

Conclusions

The limited, though intriguing, molecular evidence available suggests that there is a direct relationship between dispersal potential/distance and maintenance of homogenous genetic population structure. Haplotype diversity increases where dispersal distance is reduced below population distance or is less frequent overall as a consequence of irregular or less frequent reproductive events. Cryptic speciation is commonly found in brooding species, but is

also apparent in cases in which pelagic larval stages are of short duration. Cryptic speciation may be the result of a wide geographic range (e.g., circum-Antarctic) of a species-complex and limited dispersal potential in brooders. However, there is evidence that population (haplotype) diversity is increased even in shallow-water (shelf-depth) inhabiting broadcasters with long-distance dispersal by means of planktotrophic larvae. The increase in haplotype diversity and cryptic speciation seen in shallow-water benthos, regardless of larval developmental mode, is a strong indicator of habitat contraction during late Cenozoic glacial periods. Whereas rapid habitat expansion following retreat of the sea ice is seen in pelagic broadcasters, brooders appear to maintain genetic differentiation at local scales, resulting in cryptic speciation.

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References

- Anger K. 2001. The biology of decapod crustacean larvae. Crustacean Issues, Vol. 14. Lisse, The Netherlands: AA Balkema.
- Anger K, Moreira G, Ismael D. 2002. Comparative size, biomass, chemical composition (C, N, H) and energy concentration of caridean shrimp eggs. *Invert Reprod Devel* 42:83–93.
- Arango CP, Soler Membrives A, Miller KJ. 2010. Genetic differentiation in the Circum-Antarctic sea spider *Nymphon australe* (Pycnogonida; Nymphonidae). *Deep-Sea Res II* 58:212–9.
- Arntz WE, Gili JM. 2001. A case for tolerance in marine ecology: let us not put out the baby with the bathwater. *Scient Mar* 65:283–99.
- Arntz WE, Thatje S, Gerdes D, Gili JM, Gutt J, Jacob U, Montiel A, Orejas C, Teixidó N. 2005. The Antarctic-Magellan connection: macrobenthos ecology on the shelf and upper slope, a progress report. *Scient Mar* 69(Suppl 2):237–69.
- Aronson RB, Thatje S, Clarke A, Peck LS, Blake DB, Wilga CD, Seibel BA. 2007. Climate change and invasibility of the Antarctic benthos. *Ann Rev Ecol Evol Syst* 38:129–54.
- Aronson RB, Thatje S, McClintock JB, Hughes KA. 2011. Anthropogenic impacts on marine ecosystems in Antarctica. Book series: year in evolutionary biology. *Annals NY Acad Sci* 1223:82–107.
- Baird HP, Miller KJ, Stark JS. 2011. Evidence of hidden biodiversity, ongoing speciation and diverse patterns of genetic structure in giant Antarctic amphipods. *Molec Ecol* 20:3439–54.
- Baird HP, Miller KJ, Stark JS. 2012. Genetic population structure in the Antarctic benthos: insights from the widespread amphipod, *Orchomenella franklini*. *PLoS One* 7:e34363.
- Barber HN, Dadswell HE, Ingle HD. 1959. Transport of driftwood from South America to Tasmania and Macquarie Island. *Nature* 184:203–4.
- Bargelloni L, Marcato S, Zane L, Patarnello T. 2000. Mitochondrial phylogeny of notothenioids: a molecular approach to Antarctic fish evolution and biogeography. *Syst Biol* 49:114–29.
- Barnes DKA. 2002. Invasions by marine life on plastic debris. *Nature* 416:808–9.
- Beu AG, Griffin M, Maxwell PA. 1997. Opening of Drake Passage gateway and late Miocene to Pleistocene cooling reflected in Southern Ocean molluscan dispersal: evidence from New Zealand and Argentina. *Tectonophysics* 281:83–97.
- Brandão SN, Sauer J, Schon I. 2010. Circumantarctic distribution in Southern Ocean benthos? A genetic test using the genus *Macroscapha* (Crustacea, Ostracoda) as a model. *Molec Phyl Evol* 55:1055–69.
- Brandt A. 1991. Colonization of the Antarctic shelf by the Isopoda (Crustacea, Malacostraca). *Rep Polar Mar Res* 113:1–240.
- Brandt A. 1992. Origin of Antarctic Isopoda (Crustacea, Malacostraca). *Mar Biol* 113:15–23.
- Brandt A, Gooday AJ, Brandao SN, Brix S, Brokeland W, Cedhagen T, Choudhury M, Cornelius N, Danis B, De Mesel I, et al. 2007. First insights into the biodiversity and biogeography of the Southern Ocean deep sea. *Nature* 447:307–11.
- Brey T, Dahm C, Gorny M, Klages M, Stiller M, Arntz WE. 1996. Do Antarctic benthic invertebrates show an extended level of eurybathy? *Antarct Sci* 8:3–6.
- Brito TAS, Tyler PA, Clarke A. 1997. Reproductive biology of the Antarctic octocoral *Thouarella variabilis* Wright and Studer 1989. *Proceeding of the 6th International Conference on Coelenterate Biology, 1995*, p. 63–9.
- Bruns T. 1992. (In German) Experimentelle Untersuchungen zur Larvalentwicklung antarktischer Garnelen (Experimental studies of the larval development of Antarctic shrimp). Diploma thesis. Germany: University of Osnabrück. p. 1–129.
- Chen LB, DeVries AL, Cheng CHC. 1997. Evolution of anti-freeze glycoprotein gene from a trypsinogene in Antarctic notothenioid fish. *Proc Nat Acad Sci USA* 94:3811–6.
- Clarke A. 1992. Reproduction in the cold: Thorson revisited. *Invert Reprod Develop* 22:175–84.
- Clarke A, Crame JA. 1989. The origin of the Southern Ocean marine fauna. In: Crame JA, editor. *Origins and evolution*

- of the Antarctic biota. *The Geol Soc Spec Publ* 47:253–68. London.
- Clarke A, Crame JA. 2010. Evolutionary dynamics at high latitudes: speciation and extinction in polar marine faunas. *Phil Trans Roy Soc B* 365:3655–66.
- Clarke A, Johnston NM. 2003. Antarctic marine benthic diversity. *Oceanogr Mar Biol Ann Rev* 41:47–114.
- Coombs DS, Landis CA. 1996. Pumice from the South Sandwich eruption of March 1962 reaches New Zealand. *Nature* 209:289–90.
- Crame JA. 1999. An evolutionary perspective on marine faunal connections between southernmost South America and Antarctica. *Scient Mar* 63(Suppl 1):1–14.
- Dayton PK. 1989. Interdecadal variation in an Antarctic sponge and its predators from oceanographic climate shifts. *Science* 245:1484–6.
- Dayton PK, Oliver JS. 1977. Antarctic soft-bottom benthos in oligotrophic and eutrophic environments. *Science* 197:55–8.
- Dell RK. 1972. Antarctic benthos. *Adv Mar Sci* 10:1–216.
- Domaneschi O, da Silva J, Neto LRP, Passos FD. 2002. New perspectives on the dispersal mechanisms of the Antarctic brooding bivalve *Mysella charcoti* (Lamy, 1906). *Polar Biol* 25:538–41.
- Edwards R. 2006. Sea levels: change and variability during warm intervals. *Prog Phys Geogr* 30:785–96.
- Gallardo CS, Penchaszadeh PE. 2001. Hatching mode and latitude in marine gastropods: revisiting Thorson's paradigm in the Southern Hemisphere. *Mar Biol* 138:547–52.
- Glorioso PD, Piola AR, Leben PR. 2005. Mesoscale eddies in the Subantarctic Front, southwest Atlantic. *Scient Mar* 69:7–15.
- Gonzalez-Wevar CA, David B, Poulin E. 2011. Phylogeography and demographic inference in *Nacella (Patinigera) concinna* (Strebel, 1908) in the Western Antarctic Peninsula. *Deep-Sea Res II* 58:220–9.
- Grant RA, Griffith HJ, Steinke D, Wadley V, Linse K. 2011. Antarctic DNA barcoding: a drop in the ocean? *Polar Biol* 34:775–80.
- Griffiths HJ. 2010. Antarctic marine biodiversity – what do we know about the distribution of life in the Southern Ocean? *PLoS One* 5:e11683.
- Gutt J, Piepenburg D. 2003. Scale-dependent impact on diversity of Antarctic benthos caused by grounding of icebergs. *Mar Ecol Prog Ser* 253:77–83.
- Gutt J, Sirenko BI, Smirnov IS, Arntz WE. 2004. How many macrozoobenthic species might inhabit the Antarctic shelf? *Antarct Sci* 16:11–6.
- Hain S, Arnaud PM. 1992. Notes on the reproduction of high-Antarctic molluscs from the Weddell Sea. *Polar Biol* 12:303–12.
- Hall S, Thatje S. Forthcoming 2012. The effect of temperature on reproductive traits in a globally-distributed family of marine invertebrate (Crustacea: Decapoda: Lithodoidea). *PLoS One*.
- Heimeier D, Lavery S, Sewell MA. 2010. Molecular species identification of *Astrotoma agassizii* from planktonic embryos: further evidence for a cryptic species complex. *J Hered* 101:7755–779.
- Held C. 2003. Molecular evidence for cryptic speciation within the widespread Antarctic crustacean *Ceratoserolis trilobitoides* (Crustacea, Isopoda). In: Huiskes AH, Gieskes WWC, Rozema J, Schorno RML, van der Vies SM, Wolff WJ, editors. *Antarctic Biology in a Global Context*. Kerkwerve, The Netherlands: Backhuys Publishers. p. 135–9.
- Held C, Wägele JW. 2005. Cryptic speciation in the giant Antarctic isopod *Glyptonotus antarcticus* (Isopoda: Valvifera: Chaetiliidae). *Scient Mar* 69:175–81.
- Helmuth B, Veit RR, Holberton R. 1994. Long-distance dispersal of a Sub-Antarctic brooding bivalve (*Gaimardia trapesina*) by kelp rafting. *Mar Biol* 120:421–6.
- Hemery LG, Eleaume M, Roussel V, Ameziane N, Gallut C, Steinke D, Cruaud C, Couloux A, Wilson NG. 2012. Comprehensive sampling reveals circumpolarity and sympatry in seven mitochondrial lineages of the Southern Ocean crinoid species *Promachocrinus kerguelensis* (Echinodermata). *Molec Ecol* 21:2502–18.
- Higgs ND, Reed AJ, Hooke R, Honey DJ, Heilmayer O, Thatje S. 2009. Growth and reproduction in the brooding Antarctic bivalve, *Adacnarca nitens* (Phylobridae) from the Ross Sea. *Mar Biol* 156:1073–81.
- Highsmith RC. 1985. Floating and algal rafting as potential dispersal mechanisms in brooding invertebrates. *Mar Ecol Prog Ser* 25:169–79.
- Hoffman JI, Clarke A, Clark MS, Fretwell P, Peck LS. 2012. Unexpected fine-scale population structure in a broadcast-spawning Antarctic marine mollusc. *PLoS One* 7:e32415.
- Hoffman J, Clarke A, Linse K, Peck LS. 2011a. Effects of brooding and broadcasting reproductive modes on the population genetic structure of two Antarctic gastropod molluscs. *Mar Biol* 158:287–96.
- Hoffman JI, Peck LS, Linse K, Clarke A. 2011b. Strong population genetic structure in a broadcast-spawning Antarctic marine invertebrate. *J Hered* 102:55–66.
- Hunter RL, Halanych KM. 2008. Evaluating connectivity in the brooding brittle star *Astrotoma agassizii* across Drake Passage in the Southern Ocean. *J Hered* 99:137–48.
- Hunter RL, Halanych KM. 2010. Phylogeography of the Antarctic planktotrophic brittle star *Ophionotus victoriae* reveals genetic structure inconsistent with early life history. *Mar Biol* 157:1639–704.
- Huybrechts P. 2002. Sea-level changes at the LGM from ice-dynamic reconstructions of the Greenland and Antarctic ice sheets during the glacial cycles. *Quat Sci Rev* 22:203–31.
- Janosik AM, Mahon AR, Halanych KM. 2011. Evolutionary history of Southern Ocean *Odontaster* sea star species (Odontasteridae; Asteroidea). *Polar Biol* 34:576–86.
- Janosik AM, Mahon AR, Scheltema RS, Halanych KM. 2008. Life history of the Antarctic sea star *Labidiaster annulatus* (Asteroidea: Labidiasteridae) revealed by DNA barcoding. *Antarct Sci* 20:563–4.
- Krabbe K, Leese F, Mayer C, Tollrian R, Held C. 2009. Cryptic mitochondrial lineages in the widespread pycnogonid *Colossendeis megalonyx* Hoek, 1881 from Antarctic and Subantarctic waters. *Polar Biol* 33:281–92.
- Lambeck K, Chappell J. 2001. Sea level change through the Last Glacial Cycle. *Science* 292:679–85.
- Lambeck K, Esat TM, Potter EK. 2002. Links between climate and sea levels for the past three million years. *Nature* 419:199–206.

- Lawyer LA, Gagagan LM, Coffin FM. 1992. The development of paleoseaways around Antarctica. *Ant Res Ser* 56:7–30.
- Ledoux JB, Tarnowska K, Gérard K, Lhuillier E, Jacquemin B, Weydmann A, Féral JP, Chenuil A. 2012. Fine-scale spatial genetic structure in the brooding sea urchin *Abatus cordatus* suggests vulnerability of the Southern Ocean marine invertebrates facing global change. *Polar Biol* 35:611–23.
- Lee JE, Chown SL. 2009. Temporal development of hull-fouling assemblages associated with an Antarctic supply vessel. *Mar Ecol Prog Ser* 386:97–105.
- Leese F, Grawal S, Held C. 2010. Long-distance island hopping without dispersal stages: transportation across major zoogeographic barriers in a Southern Ocean isopod. *Naturwissenschaften* 97:583–94.
- Leese F, Held C. 2008. Identification and characterization of microsatellites from the Antarctic isopod *Ceratoserolis trilobitoides*: nuclear evidence for cryptic species. *Conserv Genet* 9:1369–72.
- Linse K, Cope T, Lörz AN, 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* 30:1059–68.
- Lörz AN, Held C. 2004. A preliminary molecular and morphological phylogeny of the Antarctic Epimeriidae and Iphimediidae (Crustacea, Amphipoda). *Molec Phyl Evol* 31:4–15.
- Lörz AN, Maas EW, Linse K, Coleman CO. 2009. Do circum-Antarctic species exist in peracarid Amphipoda? A case study in the genus *Epimeria* Costa, 1851 (Crustacea, Peracarida, Epimeriidae). *Zookeys* 18:91–128.
- Lyle M, Gibbs S, Moore TC, Rea DK. 2007. Late Oligocene initiation of the Antarctic circumpolar Current: evidence from the South Pacific. *Geology* 8:691–4.
- Mahon AR, Arango CP, Halanych KM. 2008. Genetic diversity of *Nymphon* (Arthropoda: Pycnogonida: Nymphonidae) along the Antarctic Peninsula with a focus on *Nymphon australe* Hodgson 1902. *Mar Biol* 155:315–23.
- Mahon AR, Thornhill DJ, Norenburg JL, Halanych KM. 2010. DNA uncovers Antarctic nemertean biodiversity and exposes a decades-old case of asymmetric inventory. *Polar Biol* 33:193–202.
- Meredith MP, King JC. 2005. Rapid climate change in the ocean west of the Antarctic Peninsula during the second half of the 20th century. *Geophys Res Lett* 32:L19604, doi:10.1029/2005GL024042.
- Mileikovsky SA. 1971. Types of larval development in marine bottom invertebrates, their distribution and ecological significance: a re-evaluation. *Mar Biol* 10:193–213.
- Nikula R, Fraser CI, Spencer HG, Waters JM. 2010. Circumpolar dispersal by rafting in two subantarctic kelp-dwelling crustaceans. *Mar Ecol Prog Ser* 405:2210–230.
- Page TJ, Linse K. 2002. More evidence of speciation and dispersal across the Antarctic Polar Front through molecular systematics of Southern Ocean *Limatula* (Bivalvia: Limidae). *Polar Biol* 25:818–26.
- Pearse JS. 1994. Cold-water echinoderms break Thorson's rule. In: Young CM, Eckelbarger KJ, editors. *Reproduction, larval biology and recruitment in the deep-sea Benthos*. New York: Columbia University Press. p. 27–43.
- Pearse JS, McClintock JB, Bosch I. 1991. Reproduction of Antarctic benthic marine invertebrates: tempos, modes, and timing. *Am Zool* 31:65–80.
- Pearse JS, Lockhart SJ. 2004. Reproduction in cold water: paradigm changes in the 20th century and a role for cidaroid sea urchins. *Deep-Sea Res II* 51:1533–49.
- Pearse JS, Mooi R, Lockhart SJ, Brandt A. Brooding and species diversity in the Southern Ocean: selection for brooder or speciation within brooding classes? In: Krupnik I, Lang MA, Miller SE, editors. *Smithsonian Poles Symposium*. Washington (DC): Smithsonian Inst. p. 181–96.
- Peck LS. 2002. Ecophysiology of Antarctic marine ectotherms: limits to life. *Polar Biol* 25:31–40.
- Poulin E, Feral JP. 1996. Why are there so many species of brooding Antarctic echinoids? *Evolution* 50:820–30.
- Raupach MJ, Malyutina M, Brandt A, Wägele JW. 2007. Molecular data reveal a highly diverse species flock within the munnopoid deep-sea isopod *Betamorpha fusiformis* (Barnard, 1920) (Crustacea: Isopoda: Asellota) in the Southern Ocean. *Deep-Sea Res Part II* 54:1820–30.
- Raupach MJ, Mayer C, Malyutina M, Wägele JW. 2009. Multiple origins of deep-sea Asellota (Crustacea: Isopoda) from shallow waters revealed by molecular data. *Proc Roy Soc B* 276:799–808.
- Raupach MJ, Thatje S, Dambach J, Rehm P, Misof B, Leese F. 2010. Genetic homogeneity and circum-Antarctic distribution of two benthic shrimp species in the Southern Ocean. *Mar Biol* 157:1783–97.
- Raupach MJ, Wägele JW. 2006. Distinguishing cryptic species in Antarctic Asellota (Crustacea: Isopoda) - a preliminary study of mitochondrial DNA in *Acanthaspidia drygalskii*. *Antarct Sci* 18:191–8.
- Rehm P. 2009. Cumacea (Crustacea; Peracarida) of the Antarctic shelf - diversity, biogeography, and phylogeny. *Rep Polar Mar Res* 602:1–137.
- Rogers AD, Clarke A, Peck LS. 1998. Population genetics of the Antarctic heteronemertean *Parbolasia corrugatus* from the South Orkney Islands. *Mar Biol* 131:1–13.
- Scher HD, Martin EE. 2004. Circulation in the Southern Ocean during the Paleogene inferred from neodymium isotopes. *Eart Planet Sci Lett* 228:391–405.
- Shevenell AE, Kennett JP, Lea DW. 2004. Middle Miocene Southern Ocean cooling and Antarctic cryosphere expansion. *Science* 305:1766–70.
- Stanwell-Smith D, Hood A, Peck L. 1997. A field guide to the pelagic invertebrate larvae of the maritime Antarctic. *Brit Ant Surv Cam UK*, 1–152.
- Stanwell-Smith D, Peck LS, Clarke A, Murray AWA, Todd CD. 1999. The distribution, abundance, and seasonality of pelagic marine invertebrate larvae in the maritime Antarctic. *Philos Trans R Soc Lond B Biol Sci* 354:471–84.
- Stanwell-Smith D, Peck LS. 1998. Temperature and embryonic development in relation to spawning and field occurrence of larvae of three Antarctic echinoderms. *Biol Bull* 194:44–52.
- Thatje S, Anger K, Arntz WE. 2005a. (in German) *Leben am Limit – Die Evolutionsgeschichte antarktischer Zehnfußkrebse*. *Biologie in unserer Zeit (Life at the limit: the*

- evolutionary history of Antarctic decapod crustaceans) 35:100–7.
- Thatje S, Anger K, Calcagno JA, Lovrich GA, Pörtner HO, Arntz WE. 2005b. Challenging the cold: crabs reconquer the Antarctic. *Ecology* 86:619–25.
- Thatje S, Bacardit R, Arntz WE. 2005c. Larvae of the deep-sea Nematocarinidae (Crustacea: Decapoda: Caridea) from the Southern Ocean. *Polar Biol* 28:290–302.
- Thatje S, Fuentes V. 2003. First record of anomuran and brachyuran larvae (Crustacea: Decapoda) from Antarctic waters. *Polar Biol* 26:279–82.
- Thatje S, Hillenbrand CD, Larter R. 2005d. On the origin of Antarctic marine benthic community structure. *Trends Ecol Evol* 20:534–40.
- Thatje S, Hillenbrand CD, Mackensen A, Larter R. 2008. Life hung by a thread: endurance of Antarctica fauna in glacial periods. *Ecology* 89:682–92.
- Thatje S, Mestre NC. 2010. Energetic changes throughout lecithotrophic larval development in the deep-sea lithodid crab *Paralomis spinosissima* from the Southern Ocean. *J Exp Mar Biol Ecol* 386:119–24.
- Thatje S, Schnack-Schiel S, Arntz WE. 2003. Developmental trade-offs in Subantarctic meroplankton communities and the enigma of low decapod diversity in high southern latitudes. *Mar Ecol Prog Ser* 260:195–207.
- Thornhill FJ, Mahon AR, Norenburg JL, Halanych KL. 2008. Open-ocean barriers to dispersal: a test case with the Antarctic Polar Front and the ribbon worm *Parborlasia corrugatus* (Nemertea: Lineidae). *Molec Ecol* 17:5104–17.
- Thorson G. 1936. The larval development, growth and metabolism of Arctic marine bottom invertebrates compared with those of other seas. *Meddel Grönland* 100:1–155.
- Thorson G. 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biol Rev* 25:1–45.
- Webb KE, Barnes DKA, Clark MS, Bowden DA. 2006. DNA barcoding: a molecular tool to identify Antarctic marine larvae. *Deep-Sea Res II* 53:1053–60.
- Wilson NG, Hunter RL, Lockhart SJ, Halanych KM. 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 NG, Schrödl M, Halanych KM. 2009. Ocean barriers and glaciation: evidence for explosive radiation of mitochondrial lineages in the Antarctic sea slug *Doris kerguelensis* (Mollusca, Nudibranchia). *Mol Ecol* 18:965–84.
- Zachos JC, Pagani M, Sloan L, Thomas E, Billups K. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* 292:686–93.