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*Igor Krupnik, Michael A. Lang,
and Scott E. Miller
Editors*

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Brooding and Species Diversity in the Southern Ocean: Selection for Brooders or Speciation within Brooding Clades?

John S. Pearse, Richard Mooi, Susanne J. Lockhart, and Angelika Brandt

ABSTRACT. We summarize and evaluate explanations that have been proposed to account for the unusually high number of benthic marine invertebrate species in the Southern Ocean with nonpelagic development. These explanations are divided between those involving adaptation to current conditions in this cold-water environment, selecting for nonpelagic larval development, and those involving vicariant events that either exterminated a high proportion of species with pelagic development (the extinction hypothesis) or enhanced speciation in taxa that already had nonpelagic development. In the latter case, glacial maxima over the Antarctic Continental Shelf in the Pliocene/Pleistocene glacial cycles could have created refuges where speciation occurred (the ACS hypothesis), or the powerful Antarctic Circumpolar Current passing through Drake Passage for over 30 million years could have transported species with nonpelagic development to new habitats to create new species (the ACC hypothesis). We examine the distribution and phylogenetic history of echinoderms and crustaceans in the Southern Ocean to evaluate these different explanations. We could find little or no evidence that nonpelagic development is a direct adaptation to conditions in the Southern Ocean. Some evidence supports the three vicariant hypotheses, with the ACC hypothesis perhaps the best predictor of observed patterns, both the unusual number of species with nonpelagic development and the notably high biodiversity found in the Southern Ocean.

INTRODUCTION

The unusually high incidence of parental care displayed by marine benthic invertebrates in the Southern Ocean was first noted by members of the pioneering nineteenth century expedition of the R/V *Challenger* (Thomson, 1876, 1885). Examples were found in four of the five classes of echinoderms as well as in molluscs, polychaetes, and other groups. By the end of the century, the idea was widely accepted: nonpelagic development by brooding or viviparity or within egg capsules was the dominant mode of reproduction by benthic marine animals, not only for Antarctic and subantarctic forms but also for cold-water species in general (Thomson, 1885; Murray, 1895; beautifully reviewed by Young, 1994). This notion was persuasively reinforced by Thorson (1936, 1950), who focused on gastropods in the Northern Hemisphere, and Mileikovsky (1971), who termed it “Thorson’s rule.” Both Thorson (1936) and Mileikovsky (1971), however, recognized many exceptions, and subsequently, with more information and reanalyses

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of earlier data, the generality of Thorson's rule weakened substantially (Pearse et al., 1991; Clarke, 1992; Hain and Arnaud, 1992; Pearse, 1994; Young, 1994; Stanwell-Smith et al., 1999; Arntz and Gili, 2001; Schluter and Rachor, 2001; Absher et al., 2003; Sewell, 2005; Vázquez et al., 2007; Fetzer and Arntz, 2008). We now know that many of the most abundant species in Antarctic waters, especially those in shallow water, have pelagic larvae as in other areas of the world. Moreover, taxa in the Arctic (Dell, 1972; Fetzer and Arntz, 2008) and the deep sea (Gage and Tyler, 1991) do not have the unusually high numbers of brooding species found in the Antarctic, with the exception of peracarids, all of which brood and are abundant in the Arctic and deep sea, though less diverse than in the Antarctic. Indeed, as shown by Gallardo and Penchaszadeh (2001), the incidence of brooding species of gastropods depends at least as much on the clades present in an area as on location.

Although Thorson's rule no longer applies in general terms, it was originally based on solid observations of some unusual taxa that brood in the Southern Ocean (reviewed by Pearse and Lockhart, 2004). Initially, the finding of species with nonpelagic development was attributed to adaptation to conditions peculiar to polar seas (Murray, 1895; Thorson, 1936, 1950; Hardy, 1960; Pearse, 1969; Mileikovsky, 1971). However, because high incidences of brooding occur mainly in Antarctic waters and not in the Arctic (Ludwig, 1904; Östergren, 1912; Dell, 1972), it became clear that something besides adaptation to "harsh" polar conditions had to be involved. Thorson (1936), recognizing the difference between the two polar seas, suggested that the Arctic fauna, being younger than those around the Antarctic, had not had as much time to adapt; this explanation was accepted by others (e.g., Arnaud, 1974; Picken, 1980). Nevertheless, as recognized by Dell (1972), the discrepancy between the two polar seas meant that the unusual incidence of nonpelagic development in the Southern Ocean was not likely to be the consequence of simple adaptation to some general polar conditions.

While there can be little doubt that developmental mode is influenced by, and at least initially determined by, natural selection, the adaptive nature of one particular mode over another has been subject to considerable speculation and debate (Strathmann, 1993; Havenhand, 1995; Wray, 1995; Gillespie and McClintock, 2007). Pelagic development, either with feeding or nonfeeding larvae, has usually been assumed to be plesiomorphic, and benthic development has been assumed to be derived (Jägersten, 1972; Villinski et al., 2002; Gillespie and McClintock, 2007). Moreover, once lost, planktotrophic development is rarely reacquired (Strathmann, 1978; Reid,

1990; Levin and Bridges, 1995; but see Collin et al., 2007), and this generalization probably applies to pelagic development in general. Consequently, the occurrence of benthic development in a taxon may be an adaptation to particular conditions (e.g., oligotrophic water or offshore currents), or it may be a phyletic constraint reflecting earlier adaptations that no longer apply. Paleontological evidence suggests that species of marine molluscs with nonpelagic development had smaller distributions and were more susceptible to extinction than those with pelagic development (Jablonski and Lutz, 1983; Jablonski and Roy, 2003); presumably, these had more genetically fragmented populations as well.

An alternative explanation to the unusually numerous brooding species in the Southern Ocean is that their high numbers are the consequence of populations being repeatedly fragmented, with isolated units forming new species. That is, nonpelagic development in the Southern Ocean might not reflect adaptation scattered among several clades, as it does elsewhere (e.g., Byrne et al., 2003; Collin, 2003), but rather, it may occur mainly in relatively few clades in which species proliferated. Moreover, some of these species-rich, brooding clades could contribute substantially to the unexpected high species diversity found in the Southern Ocean (Brandt et al., 2007a, 2007b; Rogers, 2007). Indeed, in some taxa, species-rich clades of brooders constitute most of the species (e.g., echinoids: Poulin and Féral, 1996; David et al., 2003, 2005; crustaceans: Brandt, 2000; Brandt et al., 2007a, 2007b). Consequently, the occurrence of many species with nonpelagic development may not be due to specific adaptations to conditions in the Antarctic but, instead, may be a consequence of isolation after vicariant events that now or in the past led to their proliferation. In this paper we evaluate and compare several adaptation versus vicariant explanations for the occurrence of species-rich clades in the high latitudes of the Southern Ocean.

PROPOSED EXPLANATIONS

ADAPTATION

Although some aspect of the current polar environment has usually been assumed to have led to the selection of nonpelagic development in the Southern Ocean, identification of the responsible agents has been elusive. The problem is compounded because unusually high numbers of brooding species are found in Antarctic and subantarctic waters but not in either the Arctic or deep sea, the other areas of the world ocean with cold water year-round. We

briefly consider below some of the ideas that have been proposed, including those that apply to cold-water environments in general.

Low Temperature

Murray (1895:1459) suggested simply that “animals with pelagic larvae would be killed out or be forced to migrate towards the warmer tropics” when temperatures cooled, to be replaced by animals without larvae existing below the “mud-line” where he thought very few animals had pelagic larvae. Similarly, Thatje et al. (2005b) argue that the predominance of developmental lecithotrophy in the Antarctic is the consequence of the near-complete extinction of benthic communities during glacial maxima and recolonization from deeper waters where species had undergone an “evolutionary temperature adaptation” that led to lecithotrophy. However, no evidence supports the idea that either nonpelagic development or lecithotrophy is an adaptation to low temperature, and the fact that a wide variety of both planktotrophic and lecithotrophic pelagic larvae have been found in both Antarctic and Arctic waters (e.g., Thorson, 1936; Stanwell-Smith et al., 1999; Sewell, 2005; Palma et al., 2007; Vázquez, 2007; Fetzer and Arntz, 2008) persuasively indicates that marine invertebrate larvae are able to survive and grow at freezing temperatures—even under high pressures found in the deep sea (Tyler et al., 2000), where many species have pelagic, planktotrophic larvae (Gage and Tyler, 1991; however, see below).

Low Temperature and Slow Development

Many studies have shown that larval development is greatly slowed at very low temperatures (e.g., Hoegh-Guldberg and Pearse, 1995; Peck et al., 2007), and the metabolic basis of this effect is gradually being sorted out (e.g., Peck, 2002; Clarke, 2003; Peck et al. 2006; Pace and Manahan, 2007). The longer larvae are in the plankton, the greater the chance that they will perish by predation or be swept away from suitable settling sites. Indeed, Smith et al. (2007) argued that lecithotrophic development might be selected because eliminating the feeding stage substantially shortens the time larvae spend in the plankton, a particular advantage for polar areas where development is slow. Going one step further, nonpelagic development eliminates loss in the plankton altogether. However, not only would this explanation apply to the cold-water environment of the Arctic and deep sea as well as to the Antarctic, but as mentioned above, many particularly abundant polar species do have slow-developing planktotrophic pe-

lagic larvae; long periods of feeding in the plankton do not necessarily appear to be selected against.

Low Temperature, Slow Development, and Limited Larval Food

Thorson (1936, 1950) developed the idea that planktotrophic larvae would be food limited in polar seas because phytoplanktonic food is available only during the summer plankton bloom, too briefly for such larvae to complete their slow development. This durable hypothesis remains current (e.g., Arntz and Gili, 2001; Thatje et al., 2003, 2005b), although little or no evidence supports it. Indeed, planktotrophic larvae of a wide range of taxa are well known in polar seas (see above). Moreover, extremely low metabolic rates of gastropod and echinoid larvae, indicative of very low food requirements, have been demonstrated by Peck et al. (2006) and Pace and Manahan (2007), respectively. There is no evidence that other planktotrophic larvae of polar seas are food limited either. In addition, this proposal is not specific to the Southern Ocean. Finally, it applies only to planktotrophic larval development, not lecithotrophic pelagic development; our concern here is pelagic and nonpelagic development, not mode of nutrition for developing embryos or larvae.

Low Adult Food Supply

Chia (1974) suggested that poor nutritional conditions for adults might favor nonpelagic development on the assumption that adults require more energy to produce the multitude of pelagic larvae needed to overcome high larval mortality in the plankton than to produce a few protected offspring. Such conditions do prevail in polar seas, where primary production is extremely seasonal (Clarke, 1988), or especially during periods of maximal multiyear sea ice and glacial expansion during the Pliocene/Pleistocene ice ages (see below). However, studies on a poecilogonous species of polychaete indicate that nutritional investment is higher in the form that produces lecithotrophic larvae than in one that produces planktotrophic larvae (Bridges, 1993), countering Chia's (1974) assumption. Moreover, even if true, the argument applies to both polar seas and is not specific to the Southern Ocean. Finally, there is little evidence that polar species are food limited over an entire year.

Large Egg Sizes

It has long been known that egg size and, presumably, energy investment into individual eggs increase with

increasing latitude (reviewed by Laptikhovsky, 2006). If more energy is allocated to each egg, fecundity is lowered. Moreover, larger eggs require more time to complete the nonfeeding phase of development than smaller eggs (Marshall and Bolton, 2007), increasing the risk of embryonic/larval mortality while in the plankton. With lower fecundity and increased risk of mortality, there could be strong selection for nonpelagic development, eliminating mortality in the plankton altogether. While the underlying reason why egg size increases with latitude remains to be understood, it could be a factor leading to nonpelagic development. However, this explanation also applies to both polar regions and not solely to the Southern Ocean.

Small Adult Size

It is also well known that taxa composed of smaller individuals tend to have nonpelagic development, while those with larger individuals tend to have planktotrophic, pelagic development (reviewed by Strathmann and Strathmann, 1982). This observation is also based on fecundity: small animals cannot produce enough offspring for any of them to have much chance of surviving the high mortality faced in the plankton. However, there are many examples of species comprised of very small individuals producing planktotrophic larvae, making generalization difficult. Nevertheless, most species in some major taxa (e.g., bivalves: Clarke, 1992, 1993) in the Southern Ocean are composed of very small individuals, so this explanation could apply to them, at least in terms of factors originally selecting for nonpelagic development.

Low Salinity

Östergren (1912) suggested that melting ice during the summer would create a freshwater layer unfavorable to pelagic larvae and therefore could be a factor selecting against them. Thorson (1936), Hardy (1960), Pearse (1969), and Picken (1980) also considered low salinity to be a factor selecting against pelagic development in polar seas. The large rivers flowing into the Arctic Ocean should make low salinity an even greater problem there than around the Antarctic. Yet, as with most of the adaptationist explanations focusing on polar conditions, the fact that nonpelagic development is less prevalent in the Arctic than in the Antarctic undermines this explanation. Thus, low salinity is not likely to be an important factor selecting for nonpelagic development in the Southern Ocean.

Narrow Shelf

Recognizing that the presence of unusually high numbers of species with nonpelagic development is mainly a feature of the Antarctic, especially the subantarctic, rather than the Arctic, Östergren (1912) also proposed that the narrow shelf and the strong winds blowing off the continent would drive larvae offshore, away from suitable settling sites. Consequently, there would be strong selection against pelagic larvae in the Antarctic but not in the Arctic. This was the first attempt to explain the high number of brooding species specifically for the Southern Ocean. However, the idea was quickly discounted by Mortensen (1913), who pointed out that it should apply as well to remote oceanic islands in the tropics, where pelagic development was already well known.

SELECTIVE EXTINCTION

Another possibility is that events in the past led to the extinction of many or most species with pelagic development in the Antarctic, leaving a disproportionate number of species with nonpelagic development. This proposal by Poulin and Féral (1994) argues that pelagic development was not adaptive, while nonpelagic development was neutral at certain times in the past in the Southern Ocean. It was developed further by Poulin and Féral (1996), Poulin et al. (2002), and Thatje et al. (2005b) and is based on the finding that during the glacial maxima of the late Quaternary ice ages, grounded ice extended to the edge of the Antarctic shelf (Clarke and Crame, 1989), obliterating most life on the shelf. During such times, thick, multiyear sea ice probably occurred year-round and extended far into the Southern Ocean surrounding the Antarctic, blocking sunlight and photosynthesis beneath it. Consequently, there would be little (only laterally advected) phytoplanktonic food to support planktotrophic larvae, and selection would be strong for lecithotrophic development, whether pelagic or benthic. Of course, primary production is necessary to support populations of juveniles and adults as well, and although massive extinction would be expected during the glacial maxima of the Pliocene/Pleistocene regardless of developmental mode, this apparently did not happen (Clarke, 1993).

Poulin and Féral (1994, 1996) suggested that selective extinction of species with planktotrophic larvae during the glacial maxima would leave behind species with nonpelagic development, but as Pearse and Lockhart (2004) pointed out, such selective extinction would leave species with both pelagic and nonpelagic lecithotrophic develop-

ment. Consequently, the selective extinction hypothesis is inadequate to explain the unusual abundance of species with nonpelagic development. However, in the case of echinoids (the taxon of concern for Poulin and Féral, 1994, 1996), there are very few species anywhere with lecithotrophic pelagic larvae—and none in the Antarctic—so the selective extinction hypothesis applies at least partly to echinoids. Similarly, the high diversity of peracarid crustaceans, most of which brood, and the paucity of decapod crustaceans, most of which have planktotrophic larvae, also may be the consequence, at least in part, of selective extinction (Thatje et al., 2003, 2005b).

Recognizing that brooding might have originated outside the Antarctic, Dell (1972), Arnaud (1974), and Picken (1980) suggested that brooding species could have colonized the Southern Ocean from elsewhere after massive extinctions, perhaps by rafting (see Thiel and Gutow, 2005). On the other hand, polar emergence from the deep sea following the retreat of multiyear sea ice in interglacial periods might have taken place for some taxa, which subsequently speciated on the Antarctic shelf (e.g., isopod families Munnopsidae, Desmosomatidae, Ischnomesidae, e.g., Brökeland, 2004; Raupach et al., 2007).

ENHANCED SPECIATION

In contrast to enhanced extinction of species with pelagic development, which would leave behind a disproportionate number of species with nonpelagic development, speciation could be enhanced by conditions in the Southern Ocean, in the past or persisting to the present, to produce species-rich clades of taxa with nonpelagic development. Nonpelagic development could have developed well before the Southern Ocean cooled, or even elsewhere altogether, but spread via a founding species to the Southern Ocean and then undergone radiation. Regardless of where or how nonpelagic development originated, if this is the case, we have not only an explanation of the unusually high number of species with nonpelagic development but also, perhaps, an explanation for the unexpected high species diversity in the Southern Ocean (Brandt et al., 2007a, 2007b; Rogers, 2007). At least two different scenarios about how this might occur are specific to the Southern Ocean.

Isolation and Speciation on the Antarctic Continental Shelf (the ACS Hypothesis)

Clarke and Crame (1989, 1992, 1997), Brandt (1991, 2000), and Thatje et al. (2005b) pointed out that during

the glacial maxima, grounded ice probably did not completely cover the shelf areas around the Antarctic continent. Instead, some isolated areas would likely be open and habitable under the ice, as seen today under ice shelves (e.g., Littlepage and Pearse, 1962; Post et al., 2007). These areas could behave as “islands” with remnants of the previously more widespread shelf fauna. Species with nonpelagic development would be effectively isolated. With the retreat of the grounded glaciers, the shelf fauna would reconnect, mixing the newly formed species as they expanded around the continent. Similar phenomena might be happening now after the disintegration of the Larsen A and B ice shelves in 2002. During the height of interglacial periods, when there was a minimum of ice cover, the Weddell and Ross seas could have been connected (Scherer et al., 1998; Thomson, 2004), further mixing species, which would be fragmented again during the subsequent glacial cycle. Clarke and Crame (1989) proposed that such repeated cycles of glacial advances and retreats over the shelf could favor speciation, and Clarke and Crame (1992, 1997) further developed this idea and suggested that such oscillation would act as a “species diversity pump.” It would be most effective, however, for species having limited dispersal capabilities, such as those with nonpelagic development.

Isolation during glacial maxima is not the only possibility for fragmenting populations on the Antarctic Continental Shelf. At present, most shallow-water habitats (<150 m) around the Antarctic continent are covered by grounded ice or floating ice shelves, and only scattered fragments of suitable habitats remain. Raguá-Gil et al. (2004) found that three such habitats, one on the west side of the Antarctic Peninsula and two others on the eastern coast of the Weddell Sea, support very different faunas. The biotas in the two habitats in the Weddell Sea differ as much from each other as they do from the one on the Antarctic Peninsula. According to Raguá-Gil et al. (2004), these differences indicate limited exchange due at least in part to a predominance of species with nonpelagic larvae. Similar differences were detected for isopod composition at sites around the Antarctic Peninsula and in the Weddell Sea (Brandt et al., 2007c). Such isolation could lead to speciation, particularly of cryptic species formed by non-selective processes (e.g., genetic drift).

Speciation of fragmented populations on the Antarctic Continental Shelf, the ACS hypothesis, would result in an increase of shelf species, so that the greatest species richness would be expected on the shelf, with decreasing richness down the slope into deeper depths. That was found to be the case for amphipods (Brandt, 2000), polychaetes

(but not isopods or bivalves) (Ellingsen et al., 2007), and many other taxa (Brandt et al., 2007a) sampled in the Atlantic sector of the Southern Ocean. In addition, because most of the glacial cycles occurred during the Pliocene and Pleistocene over only the past few million years, genetic divergence of these fragmented populations would be relatively slight, and very similar or cryptic sister species would be predicted. Molecular analyses have revealed cryptic species in isopods, which brood (Held, 2003; Held and Wägele, 2005), and a bivalve that broods (Linse et al., 2007) as well as in a crinoid, which has pelagic, lecithotrophic larvae (Wilson et al., 2007).

Isolation and Speciation via the Antarctic Circumpolar Current (the ACC Hypothesis)

Pearse and Bosch (1994) analyzed available data for mode of development in shallow-water Antarctic and subantarctic echinoderms (128 species) and found the highest proportion of species with nonpelagic development in the region of the Scotia Arc (65%), not the Antarctic continent or subantarctic islands (42% each). This pattern led them to focus on Drake Passage and the powerful Antarctic Circumpolar Current (ACC) that has been flowing through it for more than 30 million years (Thomson, 2004). They proposed that individuals of species with nonpelagic development could be rafted *infrequently* to other downstream habitats and could become established to form new isolated populations, i.e., new species. Moreover, tectonic activity in the Scotia Arc region has continually formed new habitats as crustal plates shifted, which also influenced complex eddies as water flowed through Drake Passage (Thomson, 2004). With more than 30 million years since the ACC broke through Drake Passage, many new species could form and accumulate. Pearse and Lockhart (2004) reviewed these ideas, found further support for them, and suggested ways to test them using cidaroids.

The ACC hypothesis predicts that species richness would consist of species-rich clades of taxa with nonpelagic development and would not be an accumulation of many species-poor clades with a variety of reproductive modes, including nonpelagic development, which appears to be the case (see below). Moreover, species richness would be greatest within and east of the Scotia Arc, downstream from Drake Passage. The Scotia Arc region, in fact, appears to be unusually diverse (Barnes, 2005; Barnes et al., 2006; Linse et al., 2007). Conversely, species diversity should be lower upstream, on the western side of the Antarctic Peninsula, and that is exactly the pattern Raguá-Gil et al. (2004) found in their analysis of three

shallow-water communities. Similar differences in species richness between the eastern Weddell Sea and the western coast of the Antarctic Peninsula were reported by Starbans and Gutt (2002). On a different scale, Linse et al. (2006) likewise found the highest diversity of molluscs to be in the Weddell Sea, east of the Scotia Arc, and the lowest on the western side of the Antarctic Peninsula (although this might have been due to sampling discrepancies). It can also be predicted that because the ACC hits the Antarctic Peninsula as it flows around the continent, it could carry species to the western side of the peninsula, where they might accumulate (A. Mahon, Auburn University, personal communication).

In addition, because the ACC is funneled through the whole of Drake Passage, the ACC hypothesis does not necessarily predict a depth gradient of species richness, in contrast to the ACS hypothesis. No depth gradient is seen for isopods and bivalves (Ellingsen et al., 2007). Indeed, the ACC hypothesis may account for the unexpected high species diversity recently documented for some deep-sea taxa in the Atlantic portion of the Southern Ocean (Brandt et al., 2007a, 2007b).

Finally, because the ACC continues to this day, it would not be unexpected for species to have formed, as described above, at any time over the past 30 million years, including within the past few million years, so that closely related cryptic species would be found as well as more distantly related species, all in the same clade. Unlike the ACS hypothesis, the ACC hypothesis predicts the existence of a spectrum of variously diverged species within the clades. That result is what has been found in Lockhart's (2006) analysis of brooding cidaroids, the first thorough phylogenetic analysis of a major clade of brooders within the Southern Ocean (see below).

Species with nonpelagic development are thought to be prone to high extinction rates because they typically have small population sizes and limited distributions, which make them particularly susceptible to environmental change (Jablonski and Lutz, 1983). Poulin and Féral (1994) suggested that because of such susceptibility, any enhanced speciation rate in the Southern Ocean would be countered by a high extinction rate. Consequently, they rejected an enhanced speciation model for explaining high species diversity in clades with nonpelagic development. However, with the ACC in effect for over 30 million years, the Southern Ocean has been an extraordinarily stable marine environment. Jeffery et al. (2003) proposed an idea similar to the ACC hypothesis to explain the high proportion of brooding early Cenozoic echinoids that occurred on the southern coast of Australia after Australia sepa-

rated from the Antarctic. Strong currents swept through the Tasmanian Gateway then and could have swept individuals with nonpelagic development to new habitats, where they would have potentially formed new species. McNamara (1994) earlier recognized the importance of the stability provided by the strong, constant current through the Tasmanian Gateway for favoring the accumulation of brooding echinoids; he suggested that their later disappearance was a result of the widening of the gateway and a decrease in the environmental stability. Similarly, we suggest that the ACC flowing through Drake Passage provides conditions both for enhancing speciation and for tempering extinction.

EVALUATING THE EXPLANATIONS

The proposed explanations above for the unusual abundance of species with nonpelagic development in the Southern Ocean are not mutually exclusive of each other, and one or more may apply to one or more taxa. However, with recent advances in molecular phylogenetic analyses (Rogers, 2007), these proposed explanations may be better evaluated than was possible earlier. For example, (1) if nonpelagic development is scattered within taxa found in widely distributed clades and these taxa are found both within and outside the Southern Ocean, such a mode of development is not likely to be an adaptation to conditions in the Southern Ocean. (2) If taxa with nonpelagic development in widely distributed clades are restricted to both polar environments and the deep sea, nonpelagic development might be an adaptation to cold water; if they are only in the Southern Ocean, specific conditions around the Antarctic would more likely be involved. (3) If nonpelagic development is found in all the taxa of clades found in both the Southern Ocean and elsewhere, where the basal taxa are found may indicate where the trait originated, and conditions there might be involved in the selection of nonpelagic development. (4) If nonpelagic development is found disproportionately more in Southern Ocean taxa of clades than elsewhere, either this development is a consequence of adaptation to conditions specific to the Southern Ocean, or it is the result of extinction of taxa with pelagic development. (5) If nonpelagic development is found in many taxa of clades in the Southern Ocean but only in a few taxa of basal clades found elsewhere, the Southern Ocean taxa may have proliferated because of unusual conditions there (not necessarily because nonpelagic development was adaptive). (6) If most taxa with nonpelagic development appeared only over the past few

million years, when massive glacial advances and retreats occurred, they may have been generated on the Antarctic Continental Shelf when the glacial advances separated and fragmented populations (the ACS hypothesis). (7) If the taxa appeared more or less steadily since Antarctica separated from South America, about 30 million years ago, and are most abundant in and east of the Scotia Arc, they may have been generated by infrequently rafting with the ACC to new locations (the ACC hypothesis).

SELECTED TAXA

Below we review some of the information now available for taxa of two major groups in the Southern Ocean: echinoderms and crustaceans. Species in these taxa are major components of the Southern Ocean biota, and they are relatively well known. Moreover, phylogenetic analyses are now available for some groups within them, including speciose, brooding clades. Other taxa could also be evaluated for a stronger comparative analysis, in particular, molluscs, pycnogonids, and teleosts; we hope that research is done by others.

ECHINODERMS

Nonpelagic development in echinoderms caught the attention of naturalists with the *Challenger* expedition in the nineteenth century (Thomson, 1876, 1885; Murray, 1895), setting the foundation for what became “Thorson’s rule.” Echinoderms now are among the first groups of animals in the Antarctic to have their phylogenetic relationships documented. Echinoids, in particular, are revealing. Only four major clades are present in the Southern Ocean, echinids, cidaroids, holasteroids, and schizasterids (David et al., 2003, 2005). The near absence of other clades suggests either that major extinctions have occurred or that other taxa did not find a foothold in the Southern Ocean. It is interesting to note that there are presently no clypeasteroids (sand dollars and allies) in Antarctica today, in spite of their ubiquity in cold waters both in the past and present, and that at least one species has been recorded from the Paleogene of Black Island, McMurdo Sound (Hotchkiss and Fell, 1972). Hotchkiss (1982) used this and other fossil evidence to call into question the supposed slow rate of evolution in cidaroids and any connection between the fossil Eocene faunas of Australasia and those of the so-called “Weddellian Province” of the Southern Ocean. Hotchkiss (1982:682) pointed out that any supposed “shallow-marine connection had disappeared

by middle Oligocene time because there is evidence for the deep-flowing Antarctic Circumpolar Current south of the South Tasman Rise at that time.”

Of the three major clades, there are only seven presently recognized species of echinids, all in the genus *Sterechinus*. Phylogenetic analysis using mitochondrial DNA sequences indicates that the genus diverged from *Loxechinus* in South America 24–35 million years ago, when the Antarctic separated from South America (Lee et al., 2004). Two species, *Sterechinus neumayeri* and *S. antarcticus*, are abundant and widespread around the continental shelf (Brey and Gutt, 1991). The former is known to have typical echinoid planktotrophic development (Bosch et al., 1987). The other species are less well known and are taxonomically questionable but almost certainly also have pelagic development.

Although an extensive revision is pending (see Lockhart, 2006), as of 2005, there were more than 20 recognized cidaroid taxa, and the vast majority of those have been recorded to be brooders—and present evidence (Lockhart, 2006) strongly suggests that all of them are brooders. A recent phylogenetic cladogram developed by Lockhart (2006) used fossils and a penalized likelihood analysis of CO₁, Cytochrome *b* (*Cytb*), and 18-s mitochondrial sequences to establish divergence times for the taxa of cidarids (see Smith et al., 2006, for an evaluation of using fossils for dating cladograms). The dated cladogram revealed that Southern Ocean cidaroids are monophyletic with the most likely sister taxon being the subfamily Goniocidarinae, now found in the southwest Pacific, including New Zealand and Australia, but not in the Southern Ocean. A few species of goniocidarines are known to brood, but it is not yet known whether these are sister species to the Southern Ocean clade (making goniocidarines paraphyletic). The oldest fossil goniocidarine, from the Perth Basin of Western Australia when Australia and Antarctica were connected, is more than 65 million years old, and the oldest cidaroid in the Southern Ocean clade is *Austrocidaris seymourensis*, from Eocene deposits on Seymour Island in the Scotia Arc, dated at 51 million years ago. *Austrocidaris seymourensis* had distinctive aboral brood chambers, showing that brooding was established in this clade long before cooling began. Consequently, brooding in these animals is not an adaptation to present-day conditions in the Southern Ocean.

Lockhart (2006) also showed that there are two sister clades of Southern Ocean cidaroids: the subfamily Astrocidarinae with two to three recently diverged species in a single genus (*Austrocidaris*) found in subantarctic waters on the northern edge of the Scotia Arc and the subfamily

Ctenocidarinae with more than 20 species in at least five genera found in the southern and eastern portions of the Scotia Arc and around the Antarctic Continent. Moreover, clades within the ctenocidarines diverged more or less steadily over the last 30 million years, that is, since the Antarctic Circumpolar Current was established. This pattern is precisely what the ACC hypothesis predicts.

Among the 16 species of Holasteroidea found south of the convergence, very few are found at depths less than 2000 m. Only three genera occur in relatively shallow waters: *Pourtalesia*, *Plexechinus*, and two of the three known species of *Antrechinus*. With the exception of the latter two genera, all holasteroids belong to widespread deep-sea clades that occur well north of the Southern Ocean, and none are known to have nonpelagic, lecithotrophic development. However, within *Antrechinus*, we find the most extreme form of brooding known in the Echinoidea—species that brood their young internally and “give birth” (David and Mooi, 1990; Mooi and David, 1993). The two species known to brood are found no deeper than 1500 m. The third species ascribed to *Antrechinus*, *A. drygalskii*, was only provisionally considered a plesiomorphic sister group to these remarkable brooders (Mooi and David, 1996) and occurs below 3000 m. There are no known fossil holasteroids from the Antarctic region.

There are 30 recognized species of schizasterid Spatangoida recorded by David et al. (2003, 2005) to occur in the Antarctic region. These are distributed in seven genera: *Abatus* with 11 species, *Amphipneustes* with 9, *Tripylus* with 4, *Brisaster* with 2, and *Brachysternaster*, *Delopatagus*, *Genicopatagus*, and *Tripylaster* each with a single species. Most phylogenetic analyses recognize *Brisaster* and *Tripylaster* as a monophyletic assemblage that is, at best, a sister taxon to the rest of the Antarctic Schizasteridae (Féral, et al., 1994; Hood and Mooi, 1998; Madon-Senez, 1998; David et al., 2005; Stockley et al., 2005). The ranges of *Brisaster* and *Tripylaster* are best considered subantarctic, as there is only a single record from south of 55°S, and none have been recorded in the shelf regions of the Antarctic continent. Interestingly, these genera are the only species not known to brood. All other schizasterids have nonpelagic development, brooding the young in well-developed marsupia in the aboral, ambulacral petaloid areas (Magniez, 1980; Schatt, 1988; Pearse and McClintock, 1990; Poulin and Féral, 1994; David et al., 2005; Galley et al., 2005).

The brooding schizasterids almost undoubtedly constitute a single clade (Madon-Senez, 1998; David et al., 2005). Recognizing early on the need for understanding evolutionary history to understand their phylogenies, Féral et al. (1994) compared RNA sequences in species of

the four main genera of brooding schizasterids then recognized in the Southern Ocean, supporting the monophyly of the brooding genera but partially undermining the monophyly of some of the constituent genera and therefore reinforcing the later morphological work of Madon-Senez (1998).

Fossils assigned to *Abatus*, with distinctive brood chambers, are known from the Eocene of Seymour Island on the Scotia Arc (McKinney et al., 1988). Consequently, as with the cidaroids, brooding appeared in these animals well before the Southern Seas cooled, and that mode of development cannot be attributed to polar conditions.

Poulin and Féral (1994) showed that populations of the brooding schizasterid echinoid *Abatus cordatus* in embayments around Kerguelen Island are genetically distinct, presumably because of limited gene flow. Consequently, there is genetic differentiation in these populations of brooding echinoids, and it is likely to be occurring with other brooding species with limited dispersal elsewhere in the Southern Ocean, leading to many shallow divergences in genetic structure. This is also borne out by morphological variation among specimens from different regions (Madon-Senez, 1998) and the small amounts of morphological divergence among the species themselves (David et al., 2005).

Among the brooding schizasterids, very few have ranges west of the Antarctic Peninsula. Most are distributed east of Drake Passage, along the South Shetlands and eastward through the Weddell region. For example, the genus *Amphipneustes* does not seem to occur immediately to the west of the peninsula but has abundant representation to the east of the Drake Passage, with major centers of diversity in the South Shetlands and in the region of the Weddell Sea (Figure 1). This pattern is repeated for *Abatus* and the other brooding schizasterid genera. Although sampling bias could remain a mitigating factor in the accuracy of these distributions, we do not believe that is the case for echinoids because David et al. (2003) shows that forms such as the echinids are well represented to the west of the peninsula. Even the most difficult taxa to sample, the abyssal holasteroids, are almost evenly distributed around Antarctica, with no obvious gaps in the overall distribution of this clade.

The implication is that the ranges of these brooding forms are being influenced by the prevailing ACC, which tends to force the ranges “downstream” of the Drake Passage. The precise mechanism by which brooding schizasterids are redistributed and then speciate remains unknown, but it does not overextend present data to suggest that once established, new populations of brooding forms can rapidly diverge from the originating population.

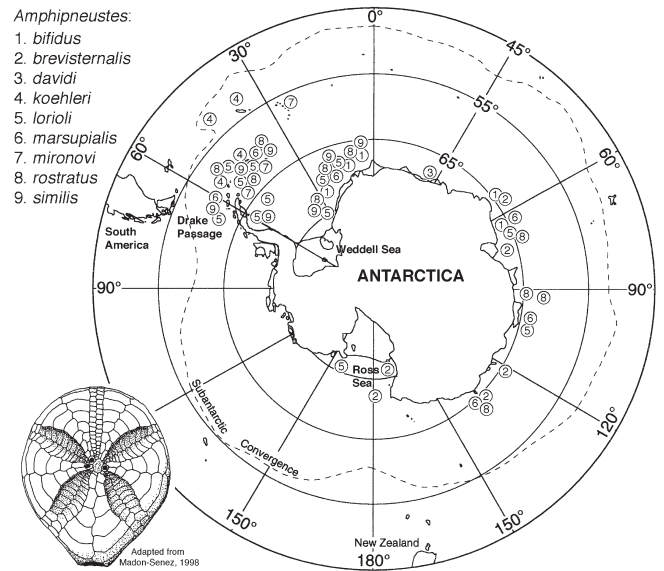


FIGURE 1. Distribution of nine species of *Amphipneustes* around Antarctica. Data were compiled from David et al. (2003) and *Polarstern* and Antarctic Marine Living Resources expeditions.

In addition to echinids, cidaroids, holasteroids, and schizasterids, there are a few other echinoid taxa known from the deeper portions of the Southern Ocean. One species of echinothurioid is known (Mooi et al., 2004); all species so far studied in this monophyletic, widespread, mostly deep-water clade have pelagic, lecithotrophic development, and the Antarctic species presumably does as well.

Unusual brooding in the Southern Ocean was also highlighted in the *Challenger* expedition reports for the other classes of echinoderms (Thomson, 1885). However, to date, there has been no phylogenetic analysis examining whether brooders belong to a few speciose clades in these classes, as is becoming evident for echinoids. In addition, members of these other classes do not have as good a fossil record, and they do not have fossilizable structures indicative of brooding, as do many echinoids. Nevertheless, if the major taxonomic groups of these classes are monophyletic, the brooding species do belong to a few speciose clades.

The majority of Southern Ocean asteroids, for example, are forcipulates in the family Asteriidae. Brooding is rare in asteriids in most of the world, limited to the speciose genus *Leptasterias* in north temperate/polar waters (Foltz et al., 2008) and several species in genera that are mainly Antarctic/subantarctic but are also found in southern South America (e.g., *Anasterias*, Gil and Zaixso,

2007; *Diplasterias*, Kim and Thurber, 2007) and southern Australia (*Smilasterias*, Rowe and Gates, 1995; Komatsu et al., 2006). However, most if not all species of asteroiids in the Southern Ocean are brooders. Arnaud (1974) lists 22 species, Pearse and Bosch (1994) list 25 species, and Clarke and Johnston (2003) report that there are approximately 37 species of asteroiids in the Southern Ocean. Foltz et al. (2007) analyzed 31 species of forcipulates using mitochondrial and nuclear sequences and found that 30 formed a clade. Only three were Southern Ocean species (*Psolidaster mordax*, *Cryptasterias turqueti*, and *Notasterias pedicellaris*), but they formed a clade within the forcipulate clade. There are 11 brooding species of asteroids on the subantarctic islands; seven of them are in the asteroiid genus *Anasterias* (Pearse and Bosch, 1994). Of the 24 species of brooding asteroids known from Antarctic waters, 18 are asteroiids, and 13 of these are in two genera, *Diplasterias* and *Lyasasterias* (Pearse and Bosch, 1994). Moreover, 19 of the 24 brooding asteroids in Antarctic waters are found in the Scotia Arc region, as would be expected from the ACC hypothesis. On the other hand, most of the genera with brooding species are circumpolar (Clark, 1962; C. Mah, Smithsonian Institution, personal communication), and it may be too early to conclude that there is a disproportional number of species in the Scotia Arc region, which has been most heavily sampled to date.

There is evidence that even brooding species of asteroids are capable of wide dispersal. *Diplasterias brucei*, for example, is not only found around the Antarctic continent and in the southern portion of the Scotia Arc but also north of the polar front on Burdwood Bank and in the Falklands Island (Kim and Thurber, 2007). Such a wide distribution by a brooding species suggests unusual capabilities of dispersal, such as by rafting. Moreover, genetic analyses would be expected to show considerable genetic differentiation, as found for *Abatus cordatus* at Kerguelen Islands (Poulin and Féral, 1994). Such analyses would be most welcome.

Although some of the asteroiid species with nonpelagic development are commonly found in the Southern Ocean, the most frequently encountered asteroids on the Antarctic shelf are species of Odontasteridae, especially *Odontaster validus*, which like the echinid echinoid *Sterechinus neumayeri*, is found around the Antarctic continent, often in very high numbers. There are about 11 species of odontasteriids in the Southern Ocean (Clarke and Johnston, 2003), two or three in the genus *Odontaster*. All, including *O. validus* (Pearse and Bosch, 1986), have pelagic development as far as is known. Consequently, as with echinoids, asteroid clades with nonpelagic development

are speciose, but most individuals are not very abundant; those with pelagic development have few species, but individuals of some species can be very abundant. Pearse et al. (1991) and Poulin et al. (2002) suggest that this difference in abundance patterns is due to ecological factors: species with pelagic development colonize and thrive in shallow areas disturbed by ice, while those with nonpelagic development occur in more stable, deeper habitats, where interspecific competition is more intense. Comparing two shallow-water habitats, Palma et al. (2007) found that an ice-disturbed habitat is dominated by *O. validus* and *S. neumayeri*, species with planktotrophic development, while a less disturbed habitat is dominated by brooding *Abatus agassizii*.

Brooding is widespread among holothurians in the Southern Ocean. Seventeen of the 41 brooding species of holothurians listed worldwide by Smiley et al. (1991) are found in Antarctic and subantarctic waters. Moreover, 15 of those species are in the order Dendrochirotida, with six each in the genera *Cucumaria* and *Psolus*, and brooding by an additional species of *Psolus* was described by Gutt (1991). In addition, 12 of the brooding species of holothuroids are found in the Scotia Arc area (Pearse and Bosch, 1994). These patterns mirror those seen in echinoids and asteroids.

Brooding is also widespread among ophiuroids in the Southern Ocean; Mortensen (1936) estimated that about 50% of the species in Antarctic and subantarctic waters are brooders. Pearse and Bosch (1994) list 33 species of brooding ophiuroids, 21 of which are found in the Scotia Arc area. Moreover, most of these species are in the most diverse families in these waters, amphiuroids, ophiacanthids, and ophiurids (Hendler, 1991). In contrast to the relatively few speciose genera with brooders in the Southern Ocean, brooding species at lower latitudes are scattered among different genera; Hendler (1991:477) suggests from this difference that there “may be selection for brooding within clades, rather than a propensity for certain clades to evolve brooding” in the Antarctic ophiuroid fauna. That is, once brooding is established in a clade, speciation is likely to occur.

There has been no phylogenetic analysis of the 12 species of Southern Ocean crinoids reported to brood, all of them occurring in the Scotia Arc region (Pearse and Bosch, 1994). However, phylogenetic analyses of *Promachocrinus kerguelensis* in the Atlantic section of the Southern Ocean revealed at least five “species-level” clades (Wilson et al., 2007). *P. kerguelensis* is found throughout Antarctic and subantarctic waters, and the one population studied, in McMurdo Sound, produces large numbers of pelagic, lecithotrophic larvae (McClintock and Pearse, 1987). Find-

ing such cryptic speciation suggests that other populations might brood or have other means of reducing dispersal.

CRUSTACEANS

Peracarid crustaceans, especially amphipods and isopods, are among the most diverse taxa in the Southern Ocean (Held, 2003; Raupach et al., 2004, 2007; Lörz et al., 2007) and are the major contributor to the high species diversity in those waters. Indeed, the extraordinary species richness of peracarids documented by recent Antarctic deep-sea benthic biodiversity (ANDEEP) cruises (Brandt et al., 2004, 2007a, 2007b) in the Atlantic sector of the deep Southern Ocean challenges the idea that a latitudinal gradient exists in the Southern Hemisphere. Moreover, molecular analyses have revealed additional cryptic species in isopods (Held, 2003; Held and Wägele, 2005; Raupach et al., 2007). All peracarids brood embryos, and most release juveniles that remain close to their parents after being released (the exceptions include exoparasitic isopods, e.g., Dajidae and Bopyridae, and pelagic forms such as mysids and hyperiid amphipods).

In contrast to the peracarids, species of decapod crustaceans, almost all of which release pelagic larvae after brooding embryos, are remarkably few in today's Southern Ocean. Only a few species of caridean shrimps inhabit the Southern Ocean, and all produce pelagic larvae, even those in the deep sea (Thatje et al., 2005a). Brachyuran crabs are important components of Patagonian benthic ecosystems (Arntz et al., 1999; Gorny, 1999), yet they are entirely absent from the Scotia Arc and Antarctic waters. Recent records of lithodid anomuran crabs in the Southern Ocean indicate a return of these crabs to the Antarctic, perhaps as a consequence of global warming, after their extinction in the lower Miocene (15 Ma) (Thatje et al., 2005b).

The dichotomy in the Southern Ocean between a scarcity of decapods, which have pelagic larvae, and a richness of peracarids, which do not have pelagic larvae, fits the extinction hypothesis (Thatje et al., 2005b). Peracarids constitute an important part of the prey of lithodid crabs (Comoglio and Amin, 1999). After the climate deteriorated in the Eocene/Oligocene and benthic decapods became extinct, the absence or scarcity of these top predators may well have created new adaptive zones, leading to a selective advantage for peracarids and favoring their diversification. Indeed, free ecological niches may have opened opportunities for spectacular adaptive radiations, as seen in some peracarid taxa (Brandt, 1999, 2005; Held, 2000; Lörz and Brandt, 2004; Lörz and Held, 2004), which were also favored because of their brooding biology.

The exceptionally high species diversity of peracarids, especially isopods in the Southern Ocean and its deep environment, cannot, however, be due simply to the fact that they are brooders without pelagic larvae. Peracarids are found throughout the world's oceans, including the Arctic. However, the Southern Ocean deep-sea samples revealed a strikingly high biodiversity (Brandt et al., 2007a, 2007b). Rather, the high diversity of peracarids in the Southern Ocean may better be accounted for by the unusual oceanographic and topographic conditions there, namely, the ACC that has been sweeping through Drake Passage for 30 million years or more. If brooding individuals have been continually displaced by that current and survive downstream in isolation from the parent population, a major "species diversity pump" would result, producing many species over time. The distribution of species in the well-studied isopod genus *Antarcturus* reveals the pattern predicted by the ACC hypothesis (Figure 2); 7 of the 15 species are found in the Scotia Arc–Weddell Sea sector, and an additional 6 are found on the coast of eastern Antarctica. Considering the extensive amount of work that has been done in the Ross Sea during the twentieth century, the bias in species richness toward the Scotia Arc–Weddell Sea and eastern Antarctic coast is unlikely to be a sampling artifact. Several other conditions may have contributed to the high diversity of peracarids in the Southern Ocean. Gaston (2000), for example, correlated high habitat heterogeneity with high diversity, and high levels of tectonic activity in

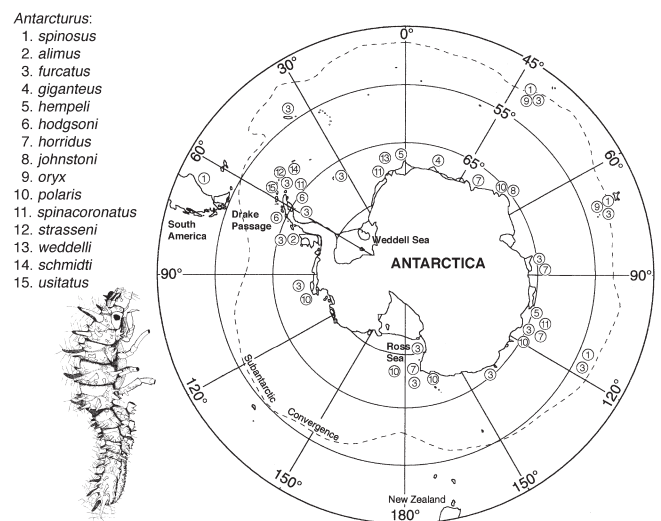


FIGURE 2. Distribution of 15 species of *Antarcturus* around Antarctica. Data were compiled from Brandt (1991), Brandt et al. (2007c), and unpublished records from *Polarstern* expeditions.

the Scotia Arc region could have produced relatively high habitat heterogeneity, although not as high as coral reef areas in lower latitudes (Crame, 2000).

Mitochondrial gene sequence analyses of iphimeriid amphipods, endemic to the Antarctic, indicate that the age of the last common ancestor of this group is approximately 34 million years (Lörz and Held, 2004), after the Southern Ocean was isolated from other fragments of Gondwanaland but well before the Pliocene-Pleistocene glacial sheets extended over the Antarctic Continental Shelf. Speciation, therefore, has probably taken place throughout the time since the ACC became established with the breakthrough of Drake Passage.

In summary, crustaceans appear to have patterns of diversity similar to those seen in echinoderms: relatively few major taxa, which are likely monophyletic clades. Some of the peracarid clades are extremely diverse and speciose, while the decapod clades present, which have pelagic development, are relatively depauperate in terms of species richness. This pattern indicates that brooding is not so much an adaptation to conditions in the Antarctic but that exceptional conditions in Antarctic waters enhance speciation of brooders.

CONCLUSIONS

1. While nonpelagic development is certainly an adaptation resulting from natural selection, it may not be an adaptation to any condition in the present-day Southern Ocean. There is no evidence that nonpelagic development is adaptive to polar conditions or, in particular, to conditions in the Southern Ocean. Instead, it may have developed in other environments long ago and is now phylogenetically constrained.

2. It is possible that most species with lecithotrophic development (pelagic as well as nonpelagic) survived periods when the Antarctic Continental Shelf was largely covered with glacial ice and the Southern Ocean was largely covered with multiyear sea ice, while most species with planktotrophic larvae went extinct because of severely reduced primary production of food for the larvae. The net effect would be (1) an increase in the proportion of species with lecithotrophic development (both pelagic and nonpelagic) and (2) an overall decrease in species richness/biodiversity. However, the Southern Ocean is notable for its high species richness/diversity.

3. Speciation could be enhanced in taxa with nonpelagic development when the following occur: (1) Refuges

form on the Antarctic Continental Shelf during the glacial maxima, fragmenting populations into small isolated units that could undergo speciation. If these formed repeatedly during the glacial-interglacial cycles of the Pliocene-Pleistocene, a “species diversity pump” would be created. This idea, termed ACS hypothesis, predicts the presence of many closely related cryptic species around the Antarctic continent, mainly at shelf and slope depths. (2) Individuals of species with nonpelagic development are infrequently carried to new habitats by the ACC flowing through the Drake Passage and over the Scotia Arc, where, if established, they form new species. Over more than 30 million years, such a process could generate many species. This idea, termed the ACC hypothesis, predicts the existence of many species in clades of varied divergence times, at a wide range of depths but with highest diversity downstream of Drake Passage, in the Scotia Arc and Weddell Sea.

4. All these possibilities appear to be important, depending on the taxon of concern, for explaining the unusual abundance of species with nonpelagic development in the Southern Ocean, but emerging data are giving most support for the ACC hypothesis. In addition, the ACC hypothesis may help account for the relatively high diversity found for many taxa in the Southern Ocean, especially in the area of the Scotia Arc and Weddell Sea.

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