

Evolutionary versus ecological success in Antarctic benthic invertebrates

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The unusually high proportion of brooding compared with broadcaster species among coastal Antarctic invertebrates has been traditionally interpreted as an adaptation to local environmental conditions. However, species with a planktotrophic developmental mode are ecologically dominant (in terms of abundance of individuals) along Antarctic coastal areas. Therefore, is the apparent ecological success of broadcasters related to their developmental mode? We argue that the present shallow Antarctic benthic invertebrate fauna is the result of two processes acting at different temporal scales. First, the high proportion of brooding species compared with coastal communities elsewhere corresponds to species-level selection occurring over geological and evolutionary times. Second, the ecological dominance of broadcasters is the result of processes operating at ecological timescales that are associated with the advantage of having pelagic larvae under highly disturbed conditions.

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Developmental modes in marine invertebrates can be classified on criteria related to the niche occupied by their offspring, such as the spatial location (benthic versus pelagic), trophic types (feeding versus nonfeeding) and degree of parental care (free versus protected) [1–3]. Within this spectrum, PLANKTOTROPHY (see Glossary) is the most conspicuous of these developmental modes [4–6]. Although less abundant, PELAGIC LECITOTROPHY and BROODING are also common. By the end of the 19th century, naturalists had noticed the great number of invertebrates species with nonpelagic development in Antarctica [7,8], and THORSON'S RULE was developed to explain this observation [9]. In spite of the incomplete, or even questionable, information regarding the developmental mode of Antarctic marine invertebrates coupled with the ongoing debates regarding the validity of Thorson's rule [10–12], the Antarctic benthos comprises an unusually high proportion of marine invertebrates that brood their young [13] (e.g. echinoderms [14–16], particularly echinoids (Box 1); molluscs [2,17,18]; and polychaetes [19]) compared with other benthic environments. However, the high abundance of individuals of species with planktotrophic developmental mode (including several echinoderms) in shallow Antarctic

environments questions previous interpretations. Here, we provide evidence to help solve this paradigm.

Is brooding an adaptation to Antarctic environmental conditions?

Because brooding is considered a derived character (apomorphy) [20,21], and is conspicuous in many Antarctic and phylogenetically distant groups, historically, its incidence has been interpreted as being a result of ADAPTATIVE CONVERGENCE in response to polar environmental conditions. Environmental factors, such as low salinity [22], low, stable seawater temperatures [23] and a short primary productivity period [17] have been invoked as important selective agents against planktotrophy. Although these adaptative hypotheses were previously widely accepted, more recent evidence suggests that different processes are responsible [16]. Although Arctic and Antarctic marine environments are similar in terms of the environmental factors mentioned above, the Arctic benthos does not contain such a high proportion of brooding species [24]. Therefore, the environmental conditions common to both poles do not necessarily favor nonpelagic developmental modes.

Another strong piece of evidence against brooding being an adaptation to the Antarctic environment comes from the fossil record. The adaptative hypotheses suggest that, since the middle Miocene [c. 15 million years ago (Mya)], when Antarctica entered a new ice age, the polar conditions would have favored the evolution from pelagic development towards brooding forms. However, brooding species exist in the Antarctic fossil record that pre-date the cooling of the continent, and are also related to living species [25], thus invalidating such a hypothesis. Although the Antarctic fossil record is very poor, there are a few, well-documented fossils, particularly of echinoids. The fossil of one brooding schizasterid species *Abatus kieri* was discovered in the Antarctic Peninsula [26], and dated to the late Eocene (c. 42–36.6 Mya), when the climate was temperate and sea-water temperature ranged between 10°C and 12°C [25]. Another fossil of the genus *Abatus* (today a genus endemic to the Antarctic) was discovered that dated back to the tropical late Cretaceous of Madagascar (c. 83–65 Mya) [27]. Similarly, brooding cidaridoid echinoids from the late Cretaceous (Maastrichtian, c. 73–65 Mya) were discovered in both the Antarctic Peninsula [28] and the southeast Pyrenees [29]. These examples show that brooding species, belonging to the same family, or even congeneric with current Antarctic species, were present in both temperate Antarctic waters and in other temperate parts of the world. This indicates that the shift from pelagic to nonpelagic development occurred before, and independently of, the recent glacial climate that has characterized Antarctica since the mid-Miocene.

Box 1. Predominance of brooding sea urchins in Antarctic and subantarctic coastal environments

Among the 50 known coastal Antarctic sea urchins (Fig. 1), only 18% develop via a planktotrophic larval stage (yellow), at least 72% are brooders (blue), and the developmental mode of the remaining 10% is still unknown (cerise, Fig. 1a) [a]. Another remarkable pattern corresponds to the low diversity observed at the family level (Fig. 1b). Among the 25 living echinoid families, only three are represented in coastal Antarctic environments, the regular Cidaridae and Echinidae (radially symmetrical), and the irregular Schizasteridae (bilaterally symmetrical). The Schizasteridae and Cidaridae contain most of the Antarctic and Subantarctic coastal sea urchin species (45 out of 50), most of which are almost exclusively brooders (at least 36 out of 45). By contrast, the Echinidae of Antarctic and Subantarctic zones contains only five species, all from the same planktotrophic genus *Sterechinus*.

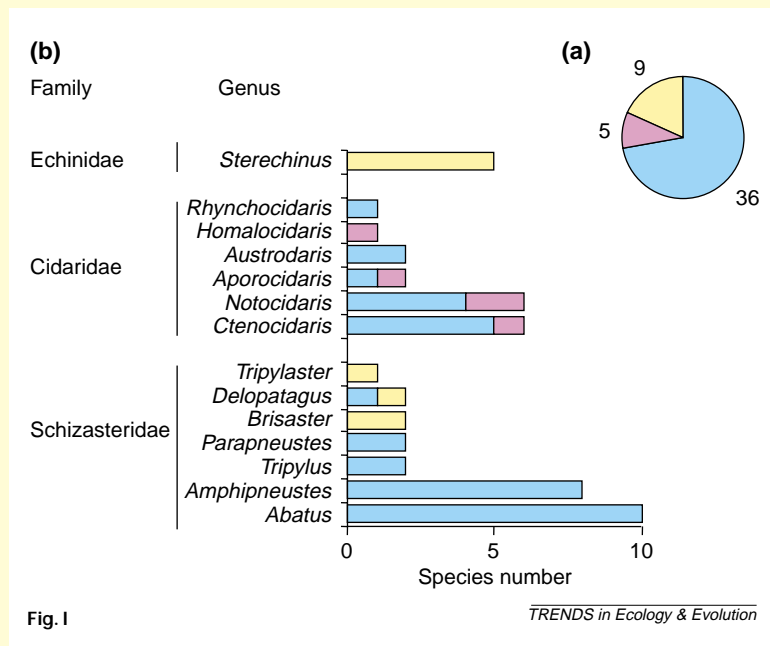


Fig. 1

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Reference

- a Poulain, E. and Féral, J.-P. (1996) Why are there so many species of brooding Antarctic echinoids? *Evolution* 50, 820–830

could have caused the local extinction of many species or even entire clades that had planktotrophic development [16,35,36]. This is exemplified by the pattern of diversity of echinoids living in Antarctic shallow environments today (Box 1). That all these species belong to only three families suggests strongly that entire taxa went extinct, particularly those with a planktotrophic developmental mode. The same pattern, characterized by high species richness and low diversity of higher taxa, is also observed among other groups, such as Antarctic holothurians [37]. An increase in the number of brooding species could have also been enhanced through VICARIANT SPECIATION [25], particularly during episodes of partial deglaciation [38]. Therefore, the high proportion of brooding species among Antarctic benthic invertebrates could correspond to a macroevolutionary trend resulting from sorting at the species level because of contrasting developmental modes experiencing differential extinction rates during adverse environmental conditions [39–41].

In spite of the high number of brooding species, the Antarctic shallow subtidal zone is dominated by numerous individuals of just a few species with a planktotrophic developmental mode, particularly echinoderms [10,11]. A quick glance into the shallow subtidal zone shows the conspicuousness of planktotrophic species, such as: the sea urchin *Sterechinus neumayeri*, described as one of the most abundant macrobenthic organisms in shallow Antarctic waters [42,43]; the asteroids *Odontaster validus*, *O. meridionalis* and *Porania antarctica* [11]; the ophiuroid *Ophionotus victoriae* [11]; the Antarctic scallop *Adamussium colbecki* [44], and the clam *Laternula elliptica* [45].

In the view of this pattern, and that Antarctica currently experiences interglacial conditions, is the apparent ecological success of these species related to the possession of a dispersive larval phase?

Is the prevalence of brooding species in Antarctica the result of species selection?

An alternative historical hypothesis, based on the different rates of extinction among taxa with pelagic versus nonpelagic developmental modes [16], considers the climatic changes that the austral region has experienced since the Miocene. This period, corresponding to the onset of a new ice age, has been characterized by the alternation of glacial and interglacial episodes, particularly during the Pleistocene (since 1.8 Mya) [30] (Box 2). During the coldest phases, the ice sheet blanketed the continental shelf and the surrounding ocean became covered by a thick layer of permanent sea-ice [31–34]. One direct consequence was a significant reduction in the amount of the light reaching the sea surface, which led to a decrease in primary productivity around Antarctica (Fig. 1). The duration of these episodes was typically much larger than the life span of organisms (in the order of thousands of years) and

Effects of ice disturbances on Antarctic shallow macrobenthos

Shallow Antarctic environments exhibit peculiar characteristics, different from those of most coastal environments elsewhere [46]. They are highly unstable environments with a high incidence of physical disturbances, ice being one of the most common [47,48]. There are diverse types of ice-related disturbance that can be summarized as: (1) the formation of ICEFOOT along the coast down to a depth of 10 m, which significantly impacts intertidal and shallow subtidal habitats during most of the year [49,50]; (2) the formation of ANCHOR ICE during winter (down to a depth of 30 m) [51]; and (3) the destructive effect of icebergs ploughing down to depths of 500 m [52,53]. These disturbances cause vertical zonation of polar shallow benthic fauna [54,55], favoring mobile species and those with pelagic larval development [56]. The occurrence of such disturbances has been recognized as an

Box 2. Important geological, climatic and tectonic events in the Southern Ocean throughout the Cenozoic

During the past 65 million years, the Earth's climate has experienced important changes, from extremes of expansive warmth with ice-free poles, to extremes of cold with massive continental ice-sheets and polar ice caps. Figure I shows a schematic representation of the changes in the Cenozoic global deep-sea oxygen isotope ($\delta^{18}\text{O}$) record (which provides a good estimation of the sea-surface temperature variations at high latitudes), and associated climatic and tectonic events [a]. The line through time in the graph corresponds to the smoothed original raw data (from [a]). From the early Oligocene to present, much of the variability (c. 70%) in the $\delta^{18}\text{O}$ record reflects changes in Antarctic and Northern Hemisphere ice volume (see [40] in [a]). The vertical bars provide a rough qualitative representation of ice volume in each hemisphere, with the pale purple bar representing periods of minimal ice coverage (<50%), and the dark purple bar representing close to maximum ice coverage (>50% of present). The late Paleocene

and early Eocene were characterized by the most pronounced warming episode of the Cenozoic that reached its maximum with the early Eocene Climatic Optimum (52–50 Mya). The long, essentially temperate Eocene (from 50 to 48 Mya to 40 to 36 Mya) was followed by a period of progressive cooling since the early Oligocene (34 Mya), which preceded the latest ice age. This cooling condition progressed gradually and was externally driven, probably by the development of the Antarctic Circumpolar Current (ACC) and Polar Front after the opening of the Drake Passage during the Oligocene (c. 30 Mya). This was followed by the rapid expansion of the Antarctic continental ice-sheets which persisted until the latter part of the Oligocene (26–27 Mya), when a warming trend reduced the extent of Antarctic ice until the middle Miocene (c. 15 Mya). The mid-Miocene Climatic Optimum episode was followed by a gradual cooling and reestablishment of a major ice-sheet on Antarctica by 10 Mya. This trend continued through the late Miocene until the early Pliocene (6 Mya), indicating additional cooling and small-scale ice-sheet expansion on west-Antarctica and in the Arctic.

It is, however, during the past 5 my that the cooling events on Earth have been more intense and frequent and the occurrence of several glacial-interglacial cycles are well recorded, particularly for the past 400 000 years (Fig. II) [b,c]. The extent of ice, estimated using changes in the amount of different isotopes of oxygen found in planktonic sea creatures, shows several major glaciation events with a 100 000-year orbitally forced ice-age cycle (a climatic response to the Earth's orbital change) [c]. (Figures modified, with permission, from [a] and [c], respectively.)

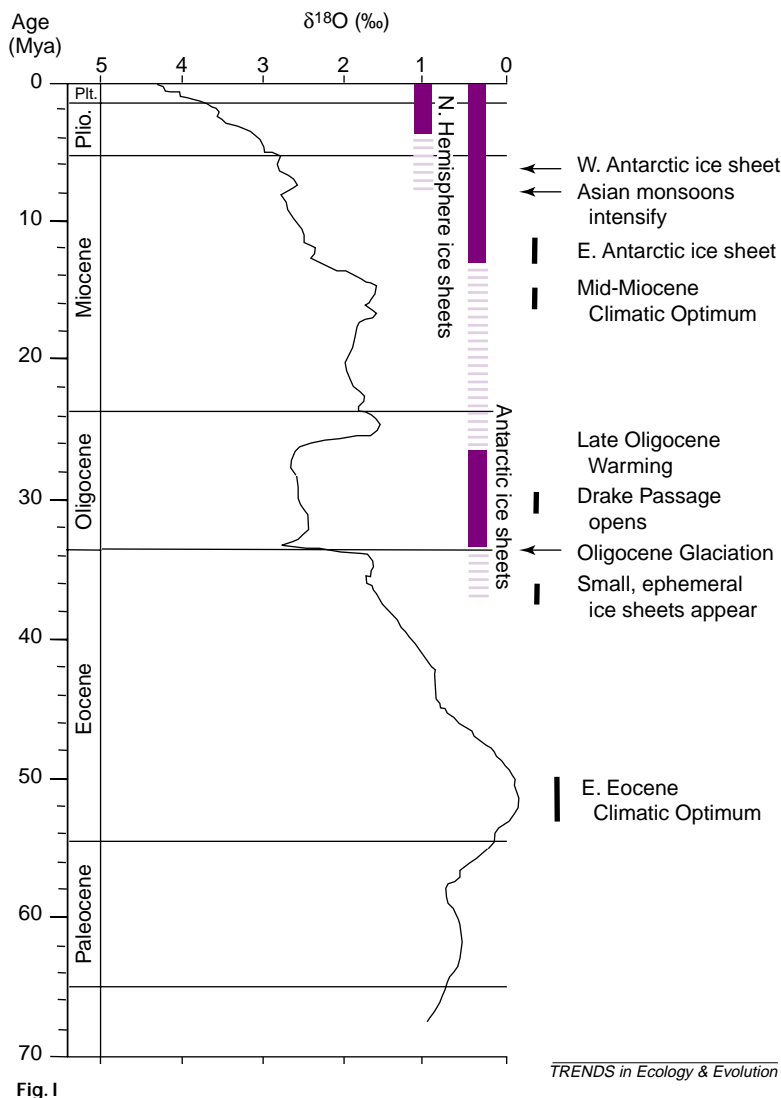


Fig. I

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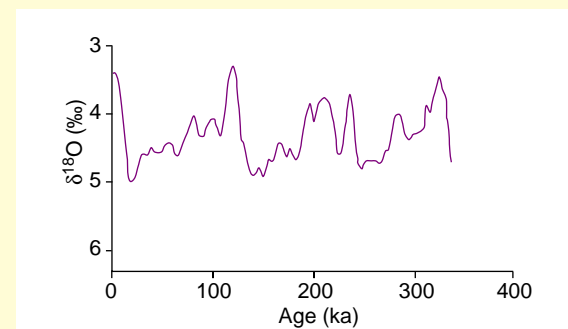


Fig. II

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important factor determining the success of different dispersal strategies. Models have also shown that habitat instability favors species with high dispersal capabilities (such as those with planktotrophic larvae), mainly through recolonization [57,58]. For marine invertebrates with reduced mobility, larvae are the main vehicles

for recolonizing recently disturbed habitats, such as typically exist after ICEBERG SCOURING events [59]. The Antarctic interglacial environmental condition is characterized by the common occurrence of disturbances and is unlikely to be favorable for brooding species in the shallow subtidal zone. In subantarctic latitudes, however, where ice impact

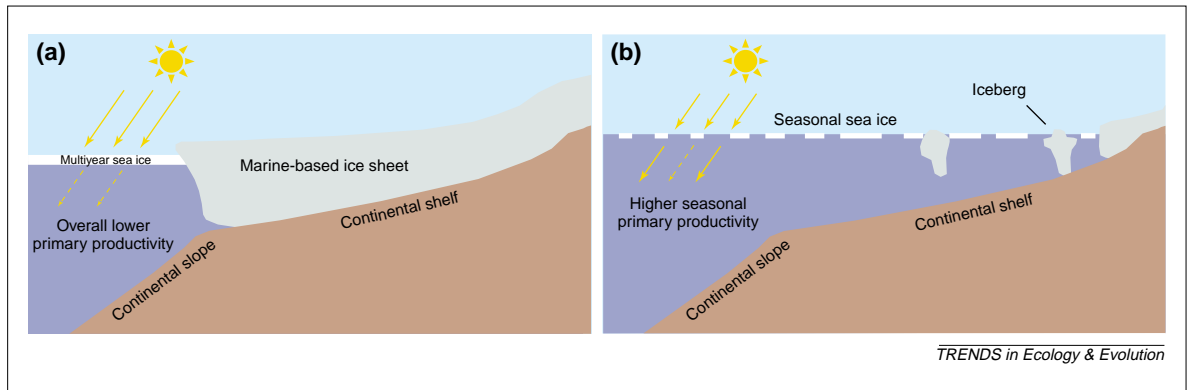


Fig. 1. Antarctic condition during the late Cenozoic glacial (a) and interglacial (b) periods. During glacial maxima, the Antarctic ice sheet covered almost the entire continental shelf. A multiyear sea-ice layer, which extended over a vast area of the surrounding sea, drastically reduced light penetration, consequently lowering primary productivity. During interglacial periods, the continental ice sheet retreated, leaving most of the continental shelf exposed. Under these conditions, icebergs were frequently carved from the continental ice shelf. During summer, fragmentation of sea ice allowed enough light penetration to enhance strong seasonal primary productivity pulses.

is less common or nonexistent, ecological dominance of planktrophic species in shallow habitats is not as evident [11].

Evolutionary success of brooding versus ecological success of planktrophs

The arguments presented here suggest that both macro- and microevolutionary processes are responsible for the biodiversity patterns of marine

invertebrates currently observed in Antarctica. On the one hand, the high number of brooding invertebrate species (evolutionary success) could be interpreted as the result of a species-sorting process operating during the coolest periods of the late Cenozoic. On the other hand, the current ecological dominance of only a few species with planktrophic development (ecological success) could be related to the capacity of their larvae to recolonize highly disturbed shallow habitats. The hypothesis of two processes acting at different timescales, as exemplified here with echinoderms, needs to be broadened to include other taxa. More detailed investigation of the developmental modes of shallow benthic invertebrates and their spatial distribution will enhance our understanding of the evolutionary and ecological processes affecting Antarctic fauna.

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Glossary

Adaptive convergence: the evolution of similar features from different ancestors.
Anchor ice: submerged ice attached or anchored to the bottom that lifts material from the bottom.
Brooding: benthic, nonfeeding, protected developmental mode.
Iceberg scouring or grounding: icebergs that plough through the sea floor in shallow waters (depth <500 meters).
Icefoot: belt or ledge of ice that forms along the shore line in polar regions.

Planktrophs: pelagic, feeding, free-swimming developmental mode.
Pelagic lecithotrophy: pelagic, nonfeeding, free-swimming developmental mode
Thorson's rule: the inferred cline of reduced pelagic larval diversity towards high latitudes
Vicariant speciation: speciation following fragmentation of distribution range

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