WHY THE DIFFERENCE IN SPECIES NUMBERS OF COASTAL ECHINOIDS IN TWO TROPHIC GROUPS AT TERRE ADELIE (ANTARCTICA): FUNCTIONAL OR HISTORICAL DIVERSITY?

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E. POULIN, J.-P. FÉRAL

Observatoire Océanologique de Banyuls, URA CNRS 2156, BP 44,
66651 Banyuls-sur-Mer cedex, France
(poulin@arago.obs-banyuls.fr, feral@arago.obs-banyuls.fr)

ECHINOID
ABATUS STERECHINUS
ANTARCTICA
FUNCTIONAL BIODIVERSITY
HISTORICAL BIODIVERSITY
BROODING
EVOLUTION

ABSTRACT. – The coastal echinoids found at Terre Adélie belong to two trophic groups. Herbivores are represented by the regular sea urchin, *Sterechinus neumayeri*, and deposit-feeders by three sympatric brooding species of *Abatus*. The coexistence of the latter is viewed in relation to long-term evolution of the clade, especially to brood protection, on the background of the tectonic and climatic history of the Antarctic continent.

OURSINS
ABATUS STERECHINUS
ANTARCTIQUE
BIODIVERSITE FONCTIONNELLE
BIODIVERSITE HISTORIQUE
INCUBATION
EVOLUTION

RÉSUMÉ. – Les oursins côtiers de Terre Adélie appartiennent à deux groupes trophiques. Les herbivores sont représentés par l'oursin régulier, *Sterechinus neumayeri*, les détritivores par trois espèces incubantes sympatriques du genre *Abatus*. La coexistence de ces dernières semble surtout liée à l'évolution à long terme du clade en relation avec le phénomène d'incubation et avec l'histoire tectonique et climatique du continent Antarctique.

The echinoids of Terre Adélie are the major coastal representatives of two different trophic groups, the herbivores and the deposit-feeders. *Sterechinus neumayeri* (Fig. 1A), an abundant regular echinoid which lives mainly on rock substrates, belongs to the first group. It grazes on diatoms and macro-algae but occasionally also on detritus and/or seal faeces (Pearse & Giese 1966). The second group includes several species of irregular echinoids of the genus *Abatus,* namely *A. ingens, A. shackletoni* and *A. nimrodi,* which remain partly or completely burrowed in muddy sediments (Fig. 1B). Two or even three species of *Abatus* are frequently found in sympatry. The simultaneous presence of these species of deposit-feeding echinoids allows one to envisage the following hypotheses :

1) The nature of the sediment offers the possibility of a differential use of the trophic resources by the various species.

2) The three deposit-feeding species illustrate the concept of functional analogues (Lawton & Brown 1993).

In this second hypothesis, the presence of these species would not be related to the functioning of the ecosystem, but would reflect the origin of echinoid diversity within Antarctica in relation to their mode of development. Indeed, in contrast to *Sterechinus neumayeri* which develops by means of a planktotrophic larva (pelagic, free and exotrophic), all the species of the genus *Abatus* are brood protecting (benthic, protected and endotrophic development).

In 1876, Thomson noticed the prevalence of non-pelagic development in benthic marine invertebrates of the Antarctic Ocean. Many studies provided support for this assumption, which became definitively established by the work of Thorson in 1950 and hence was named "Thorson's rule" by Mileikovsky (1971). It states that the frequency of pelagic development decreases from inter-tropical areas to higher latitudes, where the protected and/or benthic development prevails. For a long time unquestioned, "Thorson's rule" is seriously called in question today (Berkman *et al.* 1991; Pearse *et al.* 1991; Clarke 1992; Hain & Arnaud 1992; Pearse 1994; Féral *et al.* 1994, Pearse & Bosch 1994). Nonetheless many groups indeed show a high proportion of species with non-pelagic development in the Antarctic and sub-Antarctic zones. This is particularly true with echinoids. Among the 79 species of Antarctic and sub-Antarctic echinoids, which belong to 10 fa-
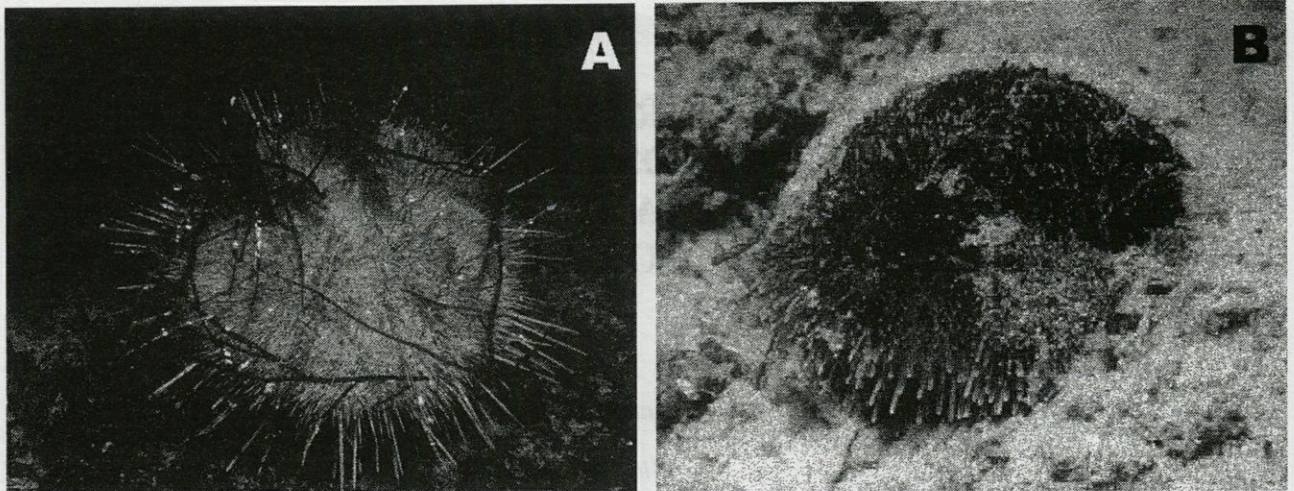
Fig. 1. – A, *Sterechinus neumayeri*, Terre Adélie, Ilot Sainte-Blanche, 20 m depth, diameter of test : 3 cm. B, *Abatus nimrodi*, Terre Adélie, Ilot Midwinter, 24 m depth, length : 4.5 cm, [photos by P. Laboute].

milies, 56 % brood their young, 34 % have planktotrophic larvae; for 10 % the developmental mode is unknown. In the coastal waters, which are most subjected to climatic variations, there are only 3 families of echinoids and the proportions of brooding species reaches 72 % (Poulin 1996).

For more than one century, scientists tried to explain the prevalence of such a development in the Antarctic Ocean and arrived at various assumptions on the significance of this phenomenon (Östergren 1912; Thorson 1950). In the majority of the cases, incubation was regarded as an adaptation to the Antarctic environmental conditions. This assumption was based on two ideas :

1, non-pelagic development evolved from the planktotrophy (Strathmann 1974, 1978; Hendler 1982; Wray & Raff 1991),

2, brooding species are widespread in the majority of the groups of marine invertebrates of the Antarctic Ocean.

The simultaneous presence of a derived character in phylogenetically distant groups was thus interpreted as the result of an evolutionary convergence. However, this conclusion is in contradiction with several observations.

1, occurrence of species with pelagic development in the Antarctic (Peck & Robinson 1994),

2, very weak representation of brood protection in the Arctic (Philip & Foster 1971; Dayton 1990),

3, existence of living or fossil species brooding in temperate and tropical seas (Emlet *et al.* 1987),

4, discovery of fossils of marsupial schizasterids of the genera *Tripylus* and *Abatus* (phylogenetically very close to the living species) that were living in temperate waters of Madagascar at the end of the Cretaceous (Lambert 1933) and of

the Antarctic Peninsula at the Eocene (McKinney *et al.* 1988).

All these observations allow one to discard the role of the polar environmental conditions in the evolution of brood protection. Thus brooding of young cannot be regarded as an adaptation to the present Antarctic environment.

The problem of the prevalence of brood-protection in the Antarctic marine invertebrates, in particular among the echinoids, actually comprises two quite different questions (Poulin 1996; Poulin & Féral 1996) :

1, What is the adaptive significance of brooding ?

2, Which are the factors responsible for the evolutionary success of brood protection within Antarctica ?

One of the principal reasons for not understanding this phenomenon was confounding these two questions, which led to an explain of the evolutionary success of brooding in Antarctica based simply on its adaptive significance. To tackle this problem, we consider the effects of brood protection on isolation and genetic differentiation between populations within a species, and thus on the processes of speciation and extinction, which are responsible for the establishment of echinoid diversity in the Antarctic Ocean.

According to the biological theory of evolution, in which genetic differentiation is the fundamental element of the process of speciation, these various modes of development must have important consequences on the modes and the rates of speciation. For species with planktotrophic development, the pelagic larvae, which are transported by marine currents for several weeks or even for

Table I. – Relationships between developmental type and geographical scale of genetic differentiation in some echinoderms.

SPECIES	DEVELOPMENT TYPE	LARVAL STAGE DURATION	SCALE OF GENETIC DIFFERENTIATION	REFERENCES
HOLOTHURIOIDEA				
Leptosynapta clarki	brooder	0	< 25 km	Hess et al., 1988
ASTEROIDEA				
Linckia laevigata	planktotrophic	28 days	> 1000 km	Williams and Benzie, 1993
Leptasterias epichlora	brooder	0	< 25 km	Kwast et al., 1990
Leptasterias hexactis	brooder	0	< 25 km	Kwast et al., 1990
ECHINOIDEA				
Arbacia punctulata	planktotrophic	56 days	> 1000 km	Marcus, 1977
Heliocidaris tuberculata	planktotrophic	20 days	> 1000 km	McMillan et al., 1992
Heliocidaris erythrogramma	pelagic lecithotrophic	4 days	100-800 km	McMillan et al., 1992
Strongylocentrotus purpuratus	planktotrophic	weeks	> 1000 km	Palumbi and Wilson, 1990
Strongylocentrotus droebachiensis	planktotrophic	weeks	> 1000 km	Palumbi and Wilson, 1990
Lytechinus variegatus	planktotrophic	50 days	> 1000 km	Rosenberg and Wain, 1982
Echinocardium cordatum	planktotrophic	weeks	> 1000 km	Féral et al., 1995
Abatus cordatus	brooder	0	< 10 km	Poulin and Féral, 1994

several months, can cover long distances and thus permit the maintenance of a gene flow between distant populations (Table I). This genetic mixing makes it possible to prevent differentiation within the species over distances on the order of a thousand of kilometers, and thus to prevent speciation. On the other hand, the brood protecting species, like those of the genus *Abatus*, have a low dispersal capacity and their populations can be genetically differentiated at separating distances of a few kilometers (Table I). Thus they speciate at much higher rates than those developing *via* pelagic larvae.

One can thus propose a first model based on different rates of speciation between the species with pelagic development and those with benthic development, to explain the prevalence of the brooding species in the Antarctic. Association between brooding and a high rate of speciation would involve a faster increase in the number of species having such a mode of development compared with the number of species with planktotrophic development.

The weakness of this model of differential rates of speciation is that it is not specific to the Antarctic areas. Indeed, it predicts the increase in the relative number of the species with non-pelagic development independently of the considered area. However, in echinoids, as in the great majority of benthic marine invertebrate groups, planktotrophic development is largely dominant in temperate and tropical areas (Emlet *et al.* 1987; Raff 1987). Thus a model which supposes that taxa consisting of species with low dispersal capacity are characterized by high rates of speciation is not satisfactory and by itself cannot explain the current prevalence of the brooding species in the Antarctic echinoids. It neglects a fundamental process in the history of taxa, namely extinction.

During the Cretaceous (135-66 Myr), Antarctica, being still connected to Australia, was characterized by a temperate and wet climate (average temperatures about 10 °C to 15 °C; Clarke & Crame 1992). The separation of Australia from Antarctica, at the end of the Eocene (~38 Myr), coincided with the beginning of a progressive cooling of the climate (Ehrmann & Mackensen 1992). Since the end of the Miocene (~6 Myr), Antarctica was a continent largely or entirely covered by ice, and was characterized by an alternation of more or less intense glacial cycles. For the coldest periods, the extension of the polar caps on the continental shelf and the persistence of the ice-barrier on vast surfaces (Grobe & Mackensen 1992), considerably reduced the quantity of light received by surface waters and entailed an important fall of the productivity around Antarctica (Siesser 1995). The decrease in primary production during the ice ages and the impossibility of a displacement of the distribution areas of species of echinoids developing through a planktonic larval phase could have involved the disappearance of the majority of them. Moreover, in contrast to the Arctic, the presence of geographical, bathymetric and hydrological barriers around the Antarctic would have strongly limited or even prevented the processes of (re)colonisation. These various factors could thus be responsible for the current prevalence of the species of brooding echinoids (Poulin 1996; Poulin & Féral 1996).

The observed low diversity at the family level tends to suggest the possibility of complete extinction of clades consisting of species with planktonic development, and thus supports the model of differential rates of extinction. The brooding species, because of their holobenthic life cycle, would thus have better resisted to the changes of the environment during the ice ages. Brood pro-

tection, a strategy emerging prior to the establishment of the current Antarctic environmental conditions, could then be regarded as a "preadaptation" *sensu* Cuénot (1932; Gayon 1995) : a character already present in an organism, a population or a species, which gives to it a selective advantage during a change of the environmental conditions.

The present diversity of Antarctic echinoids with its prevalence of the brooding species, can be interpreted as the result of a process of selection at the level of the species (Arnaud 1992; Poulin 1996), by means of differential extinction and speciation rates which are related to the respective mode of development. During the glacial cycles which characterized the evolution of the Antarctic climate during the Cenozoic, a negative selection (filtering) acting by extinction, would have resulted in the disappearance of the majority of the species with planktonic development. During the same period, a positive selection would have allowed, through the processes of speciation, the multiplication of the brooding species. This scenario, which allows one to explain the long-term tendency of increase in the relative proportion of species of brooding echinoids, thus results from the combination of the model of differential rates of extinction with that of differential rates of speciation. This new model, which is here applied to the echinoids, will have to be tested for other groups of Antarctic marine invertebrates, taking account of their specificity.

The difference of the respective number of species in two different trophic groups, at the scale of the Antarctic Ocean or merely in Terre Adélie, could thus have an origin other than the availability or the richness of trophic resources. Accordingly, it would not be related to the functioning of the coastal Antarctic ecosystem, but rather to the origin and the establishment of the diversity of echinoids in Antarctica and ultimately to the difference of the speciation / extinction ratio between species having either a pelagic or a protected development. Thus, the structure of an ecosystem is not defined solely by its instantaneous functioning, but also by the evolutionary history of the species forming part of it.

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