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BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

► CHAPTER 5.31. BIOTIC INTERACTIONS.

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THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

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5.31. Biotic Interactions

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1. Introduction

In all marine habitats, species naturally interact with other species throughout a series of different possible relationships, usually grouped under the broad category of 'biotic interactions', i.e. the interactions between living organisms.

In the ecological literature, these relationships are explained under a plethora of conceptual schemes, which differ according to the adopted criterion of classification. For example, these can be categorised according to the position of the guest (i.e. the 'symbiont') with respect to the host (topological criterion), according to the balance of benefits between the two partners (energetic criterion), or according to other points of view (see Morton 1988, Schiaparelli *et al.* 2011a). Generally speaking, it is really difficult (if not impossible) to find a synthetic and unique classification scheme, none of these criteria being exhaustive or capable to capture all nuances and exceptions.

Ideally, biotic interactions are comprised between two extreme situations, ranging from *predation* (exerted by carnivorous species, herbivores, grazers, etc.), to the partnerships usually referred to as *symbiotic interactions* or *symbioses* (e.g. commensalism, amensalism, etc.), which are less cruel and more finely tuned. It is worth remembering that the use of the term '*symbiosis*' has changed through time, shifting from the original de Bary's definition (de Bary 1878), where it just indicated the close living together of two different species, including parasitism, to a modern one where it is generally restricted only to those interactions that are mutually beneficial (Wilkinson 2001, Lincoln *et al.* 2003).

Within biotic interactions, predation is considered one of the main drivers in determining the structure of the community, both in qualitative and quantitative terms. In Antarctica, predation on benthic organisms is, however, greatly reduced. This is due partly to the extinction of selected clades of predators, elsewhere ubiquitous, and partly to dietary shifts occurred in the clades that have survived the climatic cooling phases. Most abundant predators are now slow moving organisms such as asteroids, ophiuroids, echinoids and polychaetes (Aronson & Blake 2001), which exert an important role in determining the structure of Antarctic marine benthic communities (e.g. Dayton *et al.* 1974, Bowden *et al.* 2011).

Differently from predation, symbiotic interactions have often been regarded as oddities or naturalistic curiosities, with no or negligible impact on marine communities. However, in recent years, their ecological role has been fully re-evaluated and considered to be, in some cases, of the same magnitude of predation or physical disturbance (Hay *et al.* 2004). Symbiotic interactions also represent important ecological and evolutionary drivers, often promoting speciation through host shift (e.g. Faucci *et al.* 2007).

In Antarctica, for a long time, these kinds of relationships have been considered to be absent. This fact was initially explained by the conveners of the third SCAR symposium, occurred in 1977, with the interplay of several factors, such as the lack of decapod crustaceans and the tendency of Antarctic marine species to adopt an opportunistic diet (A.A.V.V. 1977). In the last 30 years, however, a slowly growing body of ecological evidences started to accumulate, showing that symbioses *sensu de Bary*, notwithstanding an apparent overwhelming role of physical environmental factors in shaping Antarctic marine benthic communities, represent a not negligible driver of community organisation. Several papers have been published in this direction, focusing on true predation (e.g. Dayton *et al.* 1974), on epibiotic interactions (Photo 1a–b) (e.g. Gutt & Schickan 1998, Gutt 2000, Schiaparelli *et al.* 2003, Hétérier *et al.* 2008, Hardy *et al.* 2011), as well as on true cases of symbiotic interactions *sensu de Bary* (e.g. Alvaro *et al.* 2011, Lehmann *et al.* 2007, Schiaparelli *et al.* 2000, 2007, 2008, 2010, 2011b).

From a biogeographic point of view, the study of biotic interactions offers unique perspective of analysis and hints. The finding, for example, of 'asymmetries' or 'mismatches' in the biogeographic distribution of the partners of a symbiotic association, may reveal the occurrence of host-shift phenomena, likely triggered by climate-driven, local extinction of host populations. Analogously, the evaluation of the 'endemicity' of these biotic interactions, i.e. the occurrence only in the high Antarctic, or even outside the Polar Front of one or both partners, may be of help in the understanding of dispersal routes followed by species in the past and in determining the evolutionary history and duration of a 'symbiotic' relationship.

In this contribution a general account on biotic interactions occurring in Antarctica is given without any pretension of completeness and several other examples of interactions at all levels will be omitted due to space constraints.

To this group of not given examples belongs a quite large set of symbioses, which are already known to researchers but have still to be formally described from an ecological point of view (e.g. Photo 1c, d'Udekem d'Acoz & Robert 2008). The same is for the groups of parasitic crustaceans Bopyroidea and Cryptoniscoidea (internal parasites of other crustaceans) and the tiny Tantulocarida (ectoparasites of other crustaceans), which are all particularly rich in species in Antarctica, but almost unknown in respect of host preferences and incidence (e.g. Brandt *et al.* 2007, Mohrbeck *et*

al. 2010). Analogously, less obligatory interactions such as epibiotic ones, although largely represented in Antarctic waters and important in shaping the 3D structure of benthic communities (Photo 1b), will not be treated here as is for other examples of predation involving amphipods, isopods, cnidarians, carnivorous sponges, etc., which, despite being equally important from an ecological point of view in respect to 'macropredators', would represent a too long list of cases to be taken into account.

2. Biotic interactions in Antarctica

2.1. Predation

In Antarctica, studying the fossil record has principally assessed both the occurrence and intensity of predation on benthic organisms. At the macroscopic level of analysis, it emerges that predation, especially that exerted by 'durophagous' (skeleton-breaking) predators, has played a progressively decreasing role in Antarctica after the Late Eocene, due to the extinction of all clades of brachyuran crabs, lobsters, sharks and most teleosts, in coincidence of continent cooling (Aronson & Blake 2001). This major ecological shift has deeply modified the structure of past benthic communities, leading to an organisation of benthic food webs which is reminiscent of that of the Palaeozoic (i.e. has a 'retrograde' structure), when fast-moving, durophagous predators were absent and benthos was dominated by taxa not capable of skeletal breaking (Aronson & Blake 2001; Aronson *et al.* 2007).

The teleosts living today in Antarctic waters belong to notothenioids (Nototheniidae), snailfishes (Liparidae), eelpouts (Zoarcidae), rat-tails (Macrouridae) and lanternfishes (Myctophidae), which are also not durophagous. All other 'top predators', such as Weddell seals and penguins, hunt for free-swimming preys and only rarely catch benthic organisms (Aronson *et al.* 2007).

However, not all groups of benthic predators become extinct due to cooling and, in some cases, there was instead a consistent radiation and speciation in the Southern Ocean. Among Mollusca, for example, benthic predators form the top three most diverse families, with Buccinidae (generalist carnivorous predators and scavengers with about 75 species; Photo 1d) and Naticidae (bivalve shell drillers with about 35 species) having a fossil record going back to the Late Cretaceous, whilst Turridae *sensu lato* (specialised carnivorous predators, now split into 13 Families of Conoidea, see Bouchet *et al.* 2011, with about 35 species) can be traced back at least to the middle-late Eocene.

Another gastropod family, the Muricidae, whose members are among the most important group of benthic predators exerting drilling (especially on bivalves) in Antarctic waters, is also rather rich in species, most of which have been placed in the 'catch-all' genus *Trophon* Montfort, 1810. They are now included in the recently established subfamily Pagoduliniae (Barco *et al.* 2012) (Map 1). The new subfamily includes the genera *Pagodula* Monterosato, 1884, *Xymene* Iredale, 1915, *Xymenopsis* Powell, 1951, and *Trophonopsis* Bucquoy, Dautzenberg & Dollfus, 1882, whose species almost all live outside the Polar Front (Map 1, blue circles), plus the Antarctic endemic *Trophonella* Harasewych & Pastorino 2010, which is restricted within the Polar Front (Photo 1k, Map 1, red circles). The new subfamily Pagoduliniae is a strongly supported sister clade of Haustriinae, but not of Trophoninae (Map 2), which include the 'true' representatives of the genus *Trophon* (Barco *et al.* 2012).

This new analysis focused on Antarctic Muricidae also allowed a datation of speciation events, clearly (and unexpectedly) indicating a recent radiation of *Trophonella* in Antarctica during the Pliocene (Barco *et al.* 2012). Molecular data, in fact, suggest that the ancestor of this endemic genus could have 'reconquered' Antarctic shelves only after that Middle Eocene muricids, responsible of an intensive predation by drilling in the fossils of La Meseta formation, became extinct during cooling phases (Barco *et al.* 2012). The reintroduction of muricids on Antarctic shelves during the Pliocene seems to be confirmed by some major shifts occurred at the community level (Barco *et al.* 2012), such as: i) a lifestyle change in the extinct Antarctic pectinid *Austrochlamys anderssoni* (Hennig, 1911) which switched from byssate to free-living (Jonkers 2000), likely to escape muricid predation, and ii) an increased drilling predation in prey items which have never previously targeted as preys, such as the barnacle *Bathyasma corolliforme* (Hoek, 1883) and the slow-moving bivalves *Cyclocardia astartoides* (Martens, 1878) and *Thracia meridionalis* E.A. Smith, 1885, the latter two still representing the main target of extant Antarctic muricids (Jonkers 2000).

Among the few benthic mobile predators living in Antarctic waters, also octopodid cephalopods show marked 'anomalies' compared to temperate and tropical counterparts. In fact, although Antarctic octopodids produce venom containing several toxins, they do not seem to play the typical role of predators of benthic invertebrates (Undheim *et al.* 2010) and only one of these, *Pareledone turqueti* (Joubin, 1905), is known to occasionally target preys with a hard skeleton such as molluscs (Undheim *et al.* 2010). This species, despite the lack of a high dispersal potential, has a circumpolar distribution



and occurs through the whole span of the Antarctic continental shelf, down to 1000 m (Strugnell *et al.* 2012) (see Map 7 in Allcock 2013, chapter 5.12 this book). On the other hand, Antarctic cephalopods represent key species in the diet of many higher predators as penguins, seals and cetaceans (Collins & Rodhouse 2006).

In recent years, a special attention has been given to lithodid crabs (Anomura, Lithodidae, Lithodinae), living in Antarctic waters (see Maps 2–7, 9–11, 14–15 in Griffiths *et al.* 2013, chapter 5.21 this book) due to their role of crushing predators and the potential of 'reconquering' Antarctic shelves if sea-bottom temperatures will rise in the future due to global warming (Thatje *et al.* 2005). This group of decapods numbers 3 genera and 15 species (*Lithodes* Latreille, 1806, with 4 species; *Neolithodes* A. Milne-Edwards & Bouvier, 1894, with 3 species; *Paralomis* White, 1856, with 8 species) distributed all around the Antarctic continent but only where bottom temperatures are between 0.5 and 1.5°C (Hall & Thatje 2009). Below this limit, in fact, which is a physiological threshold, successful development of early life-history stages is not possible (Hall & Thatje 2009). This group of skeleton-crushing predators is now therefore absent from Antarctic shelves due to the sea-bottom temperatures below 0°C. However, it could potentially 'emerge' under modified climatic (i.e. warmer) conditions, potentially exposing the Antarctic shelf fauna to the impact of crushing predators, not experienced since the Late Eocene. In fact, it has been clearly shown that, where lithodids are present, the megafaunal diversity is greatly reduced and echinoderms are completely absent, confirming the great role of crushing-predation in shaping the overall structure of benthic marine communities (Smith *et al.* 2012). This 'invasion hypothesis', however, has been recently questioned based on an extensive compilation of both living and fossil records of lithodids, and this group could simply have persisted and radiated along Antarctic slopes (Griffiths *et al.* 2013).

2.2. 'Symbiotic' Interactions

2.2.1. Parasitic associations

Parasites are defined as those organisms (symbionts) that cause harm to another organism, the host, which the parasite utilises as habitat. Their ecological role largely overlaps with that of predators and this is also mirrored by their trophic level in stable isotopes analyses of carbon and nitrogen (e.g. Gillies *et al.* 2012). In fact, they occupy a higher trophic position in respect to that of their hosts, if they consume host tissues directly, or equivalent, if they share the same resource of the host. Although several peculiarities and differences do exist between parasitism and predation, there's now the tendency to treat the two strategies together and not as separate aspects, as it generally was in the past (see Raffel *et al.* 2008 for a detailed discussion).

Parasitic associations are by far the most widespread ones in Antarctic communities and almost all the partners involved in the different relationships belong to the dominant 'palaeozoic' clades of echinoderms and polychaetes, numerically followed by molluscs. Echinoderms usually play the role of hosts, while polychaetes and molluscs that of parasites or 'kleptocommensals'.

In Antarctic waters, all polychaetes found to live in association with other invertebrates belong to Polynoidae or 'scale-worms', a group that is well known for establishing 'symbiotic' associations in all marine environments at all latitudes (Britayev & Martin 1998). So far, at least three remarkable examples of this kind of associations have been sufficiently described from an ecological point of view.

The best-known one is that of the long-bodied polynoids which associate to various species of gorgonians (especially *Thouarella* spp.; Photo 1e) and stylasterids. This group of polychaetes has a complex taxonomical history, with several described species which turned out to be synonyms of the common *Polyeunoa laevis* McIntosh, 1885 (Barnich *et al.* 2012). This species seems to have a widespread distribution, having been found in South America, across the Polar Front and in the high Antarctic (Map 3). However, preliminary molecular data obtained in the framework of the barcoding project "BAMBI" (PNRA project 2010/A1.10, Schiaparelli *et al.*, in preparation) depict a more complex view and the existence of cryptic species having well-defined geographical ranges.

Another polynoid, *Eunoe opalina* McIntosh, 1885 (Photo 1f), represents an intriguing case of 'multitasking' species, which acts, at the same time, as parasite and predator (Schiaparelli *et al.* 2010). This scaleworm permanently lives on the holothuroid host *Bathyplotes bongraini* Vaney, 1914, digging a depression in the host tegument where it finds a shelter and accommodates its body (Schiaparelli *et al.* 2010). *E. opalina* usually lives close to the mouth of *B. bongraini* and, while being passively transported, it seems also to be able to sort and steal food collected by the host, as well as to occasionally freely move in order to hunt independently, in search for other food items not comprised within the diet of *B. bongraini* (Schiaparelli *et al.* 2010). Although the two species have been described independently, it is clear that they live in close association, despite their current distributional records (Maps 4–5) do not reflect this aspect. This fact could be due to the effect of destructive gears, which may mechanically interrupt the physical contact of the two partners, preventing the recognition of the association. It is possible that the re-examination of museum collection may be of help in reconstructing the co-occurrence of the two species at a given site, but this data integration is often just a matter of chance, most records probably remaining not compiled although potentially available on museums' shelves. There are conspicuous similarities between this Antarctic association, which occur on the Antarctic shelf at 348–555 m depth, and another one from the North Atlantic involving two very similar species, i.e. the polychaete *Eunoe laetmogonensis* Kirkegaard &

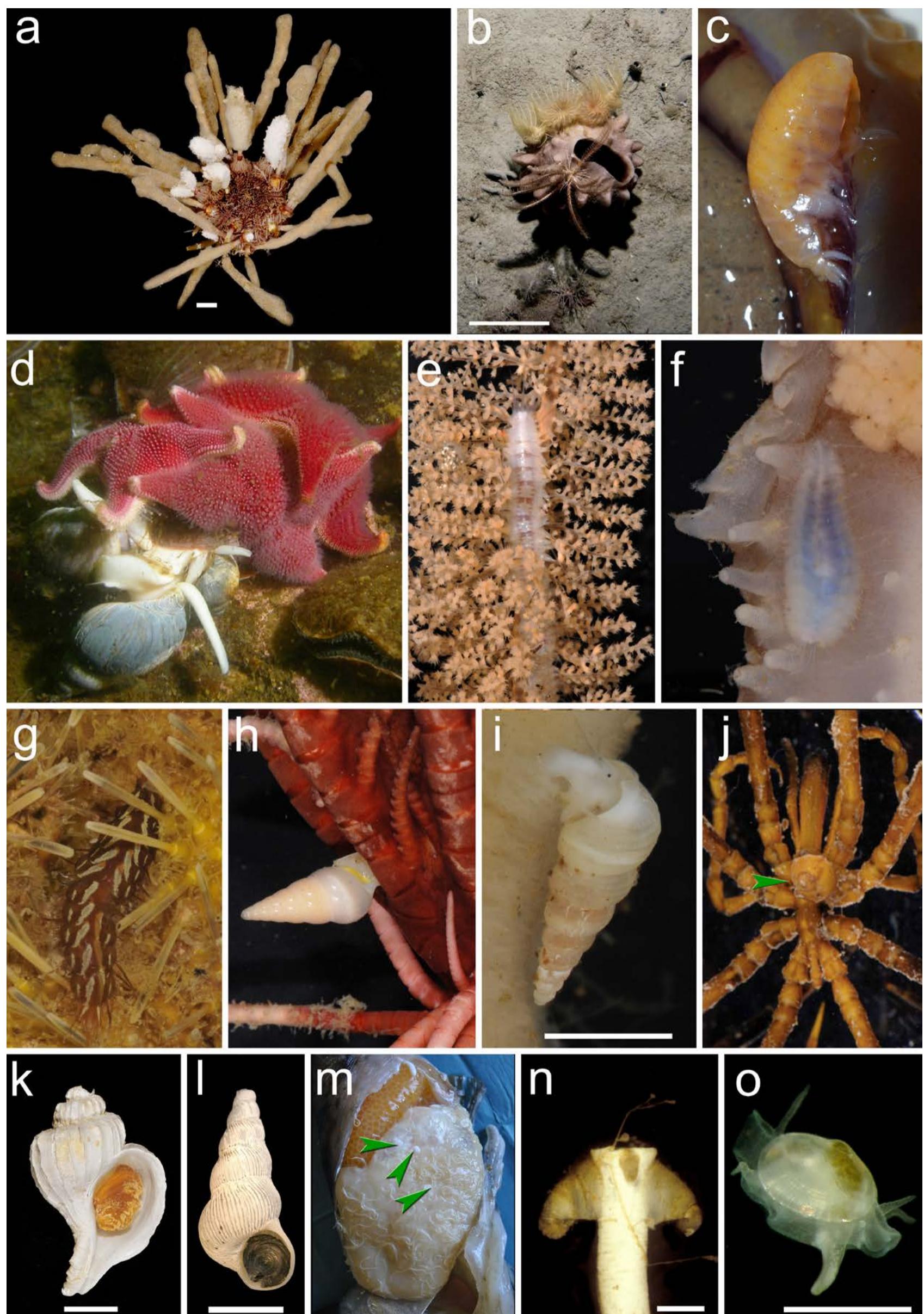
Billet, 1980 and the holothuroid *Laetmogone violacea* Theel, 1879, which live deeper (800–3200 m): considering these analogies, it is possible to speculate a common origin of the two associations although, for the moment, the lack of a molecular framework does not allow testing this hypothesis (Schiaparelli *et al.* 2010).

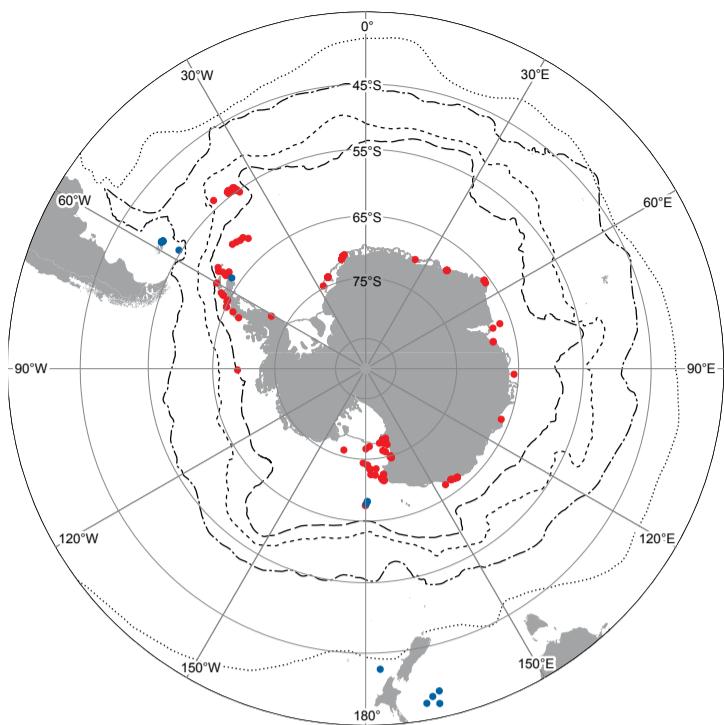
Gorekia crassicirrhis (Willey, 1902) (Photo 1g, Map 6), the third example of Antarctic associated polynoids, is the only known case of inquilistic relationship in Antarctica (Schiaparelli *et al.* 2011b). This species lives in the gut of *Abatus (Pseudabatus) nimrodi* (Koehler, 1911) in the Ross Sea and East Antarctica (Map 7), and inside *Brachysternaster chesheri* Larrain, 1985 in the Weddell Sea (Map 7) (Schiaparelli *et al.* 2011b). Since both hosts are irregular sea urchins belonging to Schizasteridae, this example is one of the several possible cases of 'host-switch' phenomena likely determined by glacial cycles, which may have made unavailable the 'typical' host of an association in some areas, forcing the symbiont to adapt to other species.

Among molluscs, there are several examples of parasites in the families of Eulimidae, Cerithiopsidae, Epitonidae and Zerotulidae.

Unfortunately, with the exception of Epitonidae and Zerotulidae, which do not comprise many species and are fairly well known and taxonomically revised groups for the Southern Ocean, the taxonomy of Cerithiopsidae and

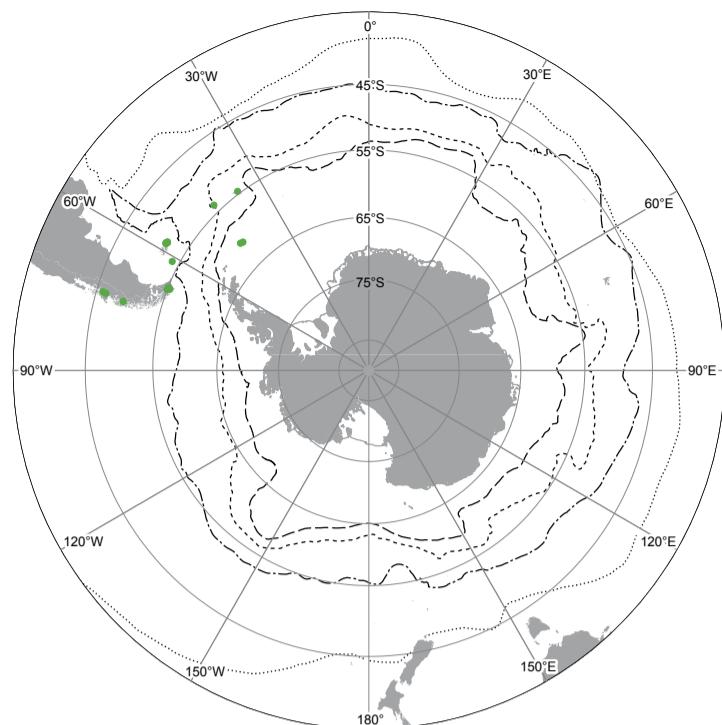
Photo 1 (a) Cidarid spines represent a very peculiar habitat where a specialised fauna of invertebrates, not found on other hard substrates (Hétérier *et al.* 2008), can take advantage of an elevated position and intercept water-carried particles. Among the most frequent invertebrates observed on the shaft of cidaroid primary spines there are holothuroids (see Massin & Hétérier 2004) belonging to the genera *Taeniogyrus* Semper, 1867 and *Echinopsolus* Gutt, 1990. On the figured cidarid, unidentified white-coloured holothuroids and several species of encrusting sponges (beige-coloured) can be recognized. Scale bar: 1 cm. Ross Sea, NIWA IPY-CAML Expedition 2008, Stn 81, image 1383. Image: Stefano Schiaparelli © NIWA. — (b) At a bigger scale, several invertebrates of large size contribute to the 3D structure of Antarctic benthic communities and constitute a secondary substrate for rheophilic species. In this picture two different species of comatulids climbed on a small *Rossella fibulata* Schulze & Kirkpatrick, 1910 in order to take advantage of a higher position and intercept food. Scale bar: 20 cm. Ross Sea, NIWA IPY-CAML Expedition 2008, Stn 55, frame 0144; DTIS seabed. Image © NIWA. — (c) Several examples of symbiotic association found in Antarctica, although known to researchers, are still to be formally described from an ecological point of view. In this picture an undescribed and blind lysianassoid *Adelieilla* Nicols, 1938 peer out the intestine loops of the holothuroids where it was found (d'Udekem d'Acoz & Robert 2008, Larsen B area). Image: Pablo J. López González © Universidad de Sevilla. — (d) Two of the most common Antarctic 'retrograde' predators (which sometimes also act as scavengers), the gastropod *Neobuccinum eatoni* (E.A. Smith, 1875) (Gastropoda, Buccinidae) and the asteroid *Odontaster validus* Koehler, 1906, caught while feasting on a dead *Adamussium colbecki* scallop (a light brown valve edge is visible between the mass of gastropods and that of asteroids). XXI PNRA Expedition, Terra Nova Bay, 4 Feb. 2006, 25 m deep. Image: Stefano Schiaparelli © PNRA. — (e) *Polyeunoa laevis* McIntosh, 1885 (Polynoidae) on a *Thouarella* sp. In order to show the polychaete, which moves along the gorgonian main axis, some branches have been cut. Ross Sea, NIWA IPY-CAML Expedition 2008, Stn 222, picture 3371c. Image: Stefano Schiaparelli © NIWA. — (f) The polynoid *Eunoe opalina* McIntosh, 1885 adhering to the host body, the holothuroid *Bathyplotes bongraini* Vaney, 1914, close to its mouth (in the top-right corner). Ross Sea, NIWA IPY-CAML Expedition 2008; Image: Stefano Schiaparelli © NIWA. — (g) The polynoid *Gorekia crassicirrhis* (Willey, 1902) crawling around the mouth of the irregular sea urchin *Abatus nimrodi* (Koehler, 1911) (Schizasteridae). MNA 2898, XXV PNRA Expedition, Terra Nova Bay, 70 m deep. Image: Stefano Schiaparelli © PNRA. — (h) A *Bathycrinicola tumidula* (Thiele, 1912) specimen (Gastropoda, Eulimidae) is parasitising the arm of a *Notocrinus virilis* Mortensen, 1917 specimen with the proboscis deeply inserted between crinoid's skeletal plates Ross Sea, NIWA IPY-CAML Expedition 2008, Stn 84, picture 1431b. Image: Stefano Schiaparelli © NIWA. — (i) The cerithiopsid 'Krachia' antarctica (E.A. Smith, 1907) (Gastropoda, Cerithiopsidae) photographed while crawling on the surface of the demosponge *Haliclona dancoi* (Topsent, 1913). Scale bar: 5mm. MNA 2717, XXV PNRA Expedition, Terra Nova Bay, 25 m deep. Image: Stefano Schiaparelli © PNRA. — (j) The zerotulid *Dickdellia labioflecta* (Dell, 1990) (Gastropoda, Zerotulidae; green arrow) adhering on the pycnocionid *Colosseides robusta* Hoek, 1881, behind the proboscis (note the mimetic colour). MNA 1355, Carbonant 2002, XVII PNRA Expedition, 389 m. Image: Stefano Schiaparelli © MNA. — (k) *Trophonella longstaffi* (E.A. Smith, 1907) (Gastropoda, Muricidae, Pagoduliniae) is one of the main benthic drilling predators at shallow depths in the Antarctic. Its 'lamellate' sculpture resembles that of the genus *Trophon*, not phylogenetically closely related (see text for details). Scale bar: 1cm. MNA 42, XVII PNRA Expedition, 15/01/2001, 10 m depth. Image: Stefano Schiaparelli © MNA. — (l) *Epitonium eltanini* (Dell, 1990) is one of the few Antarctic species of Epitonidae present in Antarctica. This family is rather rich in species in temperate and, especially, in tropical marine environments, with species specialised in parasitising hexacorals. The host of all Antarctic representatives is still unknown. Scale bar: 1cm. MNA 228, Ross Sea, NIWA BIOROSS Expedition 2004, Stn 178. Image: Stefano Schiaparelli © MNA. — (m) Liver of a female of the ice-fish *Chionodraco hamatus* (Lönnberg, 1905) heavily infested by nematoda belonging to the *Contracecum osculatum* (Rudolphi, 1802) complex (whose final host is the Weddell seal) and by diphyllobiotrid larvae (Cestoda) (arrows) (whose final hosts are sea birds and sea mammals). Specimen caught at Terra Nova Bay, XXVII PNRA Expedition. Image © Dr. Mario Santoro. — (n) Three specimens of the capulid *Capulus subcompressus* Pelseneer, 1903 adhering to the edge of a *Serpula narconensis* Baird, 1865 (Polychaeta, Serpulidae) tube. These three individuals lie at 90° from each other, in order not to be 'disturbed' during feeding by the other specimens. The central specimen is of a much smaller size and has reached the host later than the first two. Scale bar: 5mm. (XVII PNRA Expedition 2001–2002. Image: Stefano Schiaparelli © MNA. — (o) *Waldo parasiticus* (Dall, 1876) (Bivalvia, Galeommatoidea) is the unique Antarctic representative of a large family of small species of bivalves, which invariably associate with echinoderms (generally echinoids and holothuroids). The mantle edges extend far beyond the shell edge. Several Antarctic irregular sea urchins of the genus *Abatus* hosts this bivalve species, which can be found in numbers around the mouth of the host and in the brooding chambers. Scale bar: 5mm. MNA 2936, XXV PNRA Expedition, 8/01/2010, 10 m depth. Image Stefano Schiaparelli © MNA. ►





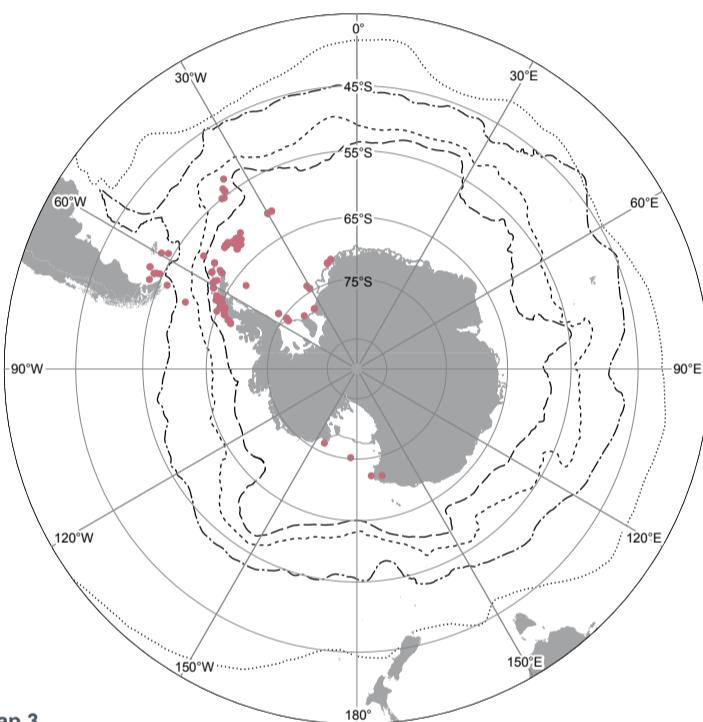
Map 1

- Records of Pagonulidae (non-endemic genera)
- Records of *Trophonella* (Antarctic endemic genus)



Map 2

- Records of *Trophon geversianus* and *Trophon plicatus*



Map 3

- *Polyeunoa laevis*

Biotic Interactions Maps 1–3 Map 1. Pagodulinae distribution. Blue dots represent distributional records of genera belonging to this subfamily but not restricted to Antarctica, including the species *Trophon cf. cuspidarioides* Powell, 1951, *Pagodula lata* B.A. Marshall & Houart, 2011, *Pagodula eos* B.A. Marshall & Houart, 2011, and *Zeatrophon pulcherimus* (Finlay, 1930) (data from Barco *et al.* 2012). The genus *Pagodula* extends far beyond Antarctic waters, from which it probably spread out during the Pliocene and can now be found around New Zealand but also in the North Atlantic and Mediterranean Sea (data not captured by the map) (see Barco *et al.* 2012 for details). Red dots represent the distribution of the Antarctic endemic genus *Trophonella*, comprising the species *T. echinolamellata* (Powell, 1951), *T. enderbyensis* (Powell, 1958), *T. longstaffi* (E.A. Smith, 1907) (Photo 1k), *T. scotiana* (Powell, 1951) and *T. shackletoni* (Hedley, 1911), whose phylogenetic position was assessed thanks to molecular data (Barco *et al.* 2012). Map 2. Trophoninae distribution: known distributional records of the species *Trophon geversianus* (Pallas, 1774) and *Trophon plicatus* (Lightfoot, 1786). Map 3. Distribution of the polynoid *Polyeunoa laevis* McIntosh, 1885 (Photo 1e), a parasite of several species of cnidarian hosts (see text for details); no molecular data are available at the moment to verify the degree of genetic distance between South American and Antarctic representatives.

Eulimidae is still in a state of flux with many putative species of uncertain status. In fact, although several species names are in use, the still not-assessed intra-specific morphological variability and an almost complete lack of knowledge about host association preferences, prevent an estimate of the exact number of extant Antarctic species in these two families.

The Eulimidae is a large family of eurybathic gastropods worldwide distributed that parasitise echinoderms, with genera specifically adapted to feed on Asteroidea, Ophiuroidea, Echinoidea, Holoturoidea and Crinoidea. Notwithstanding eulimids are very common in Antarctic benthic samples, only for two species the host is known: *Asterophila perknasteri* Warén, 1994 (which lives inside the asteroid *Perknaster* sp.) (Warén & Lewis 1994) and *Bathycrinicola tumidula* (Thiele, 1912) (Photo 1h) (which lives on the comatulid *Notocrinus virilis* Mortensen, 1917) (Schiaparelli *et al.* 2007). As in the case of *E. opalina*, and possibly due to the same reason, the two partners of this latter association show an apparent mismatch in distributional records (Maps 8–9).

Analogously to Eulimidae, even for the majority of Cerithiopsidae, which obligatorily feed on sponges, information about the hosts is lacking. The only two exceptions are *Cerithiella austrina* (Hedley, 1911), which was recorded on the sponge *Homixinella balfourensis* (Ridley & Dendy, 1886) (Arnaud 1972), and '*Krachia*' *antarctica* (E.A. Smith, 1907) (Photo 1i), which is common on the sponge *Haliclona dancoi* (Topsent, 1901) at diving depths (Schiaparelli et

al. 2003). Given the high diversity of sponges in Antarctica and the general high specificity of cerithiopsids for the host, this family could represent an important source of biogeographic information when more associational data will become available in the future.

Other gastropod families, such as the Epitonidae or "winkletraps", usually rich in species in the tropics where they parasitise hexacorals (Gittenberger & Gittenberger 2005), show a low diversity in Antarctica. So far, only three species, *Acirsa antarctica* (E.A. Smith, 1907), *Murdochella antarctica* Dell, 1990 and *Epitonium eltanini* (Dell, 1990) have been reported for the Southern Ocean, but for none of these the host is known. Moreover, in most cases, the records refer to empty shells and, as far as is known, the only species with a record of a living specimen is that of *E. eltanini* (Photo 1l) (Schiaparelli, unpublished record).

Among Antarctic parasites, the zerotulid *Dickdellia labioflecta* (Dell, 1990) (Photo 1j) represents a very special case, being the unique worldwide mollusc known to parasitise pycnogonids. *D. labioflecta*, has a life cycle largely based on the host, where it lays the eggs and the embryos complete the development (Lehmann *et al.* 2007). This species was previously (and incorrectly) considered to be endemic in the Weddell Sea, but it has been later shown to be circumpolar in distribution (Map 10) (Schiaparelli *et al.* 2008). Although only seldom recorded in benthic samples, it is highly probable that *D.*

labioflecta has a much wider diffusion, especially considering the distribution of its most common host, the pycnogonid *Colossendeis megalonyx* Hoek, 1881. However, molecular analyses suggest caution in the interpretation of the biogeography of *C. megalonyx* (Map 11), since this species is formed by at least six reciprocally monophyletic phylogenetic groups, with a clade also occurring outside the Polar Front (Krabbe et al. 2010). In the future, molecular data will help in assessing if also *D. labioflecta* is represented by a single widespread species or, on the contrary, by a mosaic of cryptic species, each one possibly having specific host preferences.

Among tanaidacean crustaceans, *Exspina typica* Lang, 1968, has been found in deep-sea elasipodid holothuroids, where the species lives in the intestine and body cavity digging tunnels into the host body wall (Alvaro et al. 2011). This tanaid (Map 12) shows an only partially overlapping distribution with that of its host (Map 13) possibly due to the fact that its minute size makes its detection very difficult in the field. However, it has been shown that it is possible to recognise the presence of the parasite even from ROV pictures due to the transparency of elasipodid body wall (Alvaro et al. 2011). It is possible that the currently known distribution of this species could be easily updated when more ROV images will be examined for this target.

In Antarctica, several examples of internal parasites (not treated in this chapter in detail) are known to occur, sometimes also showing high infestation rates (Photo 1m). Life cycles, host-specificity and geographical distribution of Antarctic Digenea, Cestoda, Nematoda and Acanthocephala, have been reviewed by Rocka (2006). Most of helminths that have their life cycles in bony fishes show a high degree of endemism (with very few examples of cosmopolitan or bipolar species) (Rocka 2006) and a generally low host specificity (Palm et al. 2007). *Anisakis* (Nematoda) infections in the high Antarctic may take place through migrating myctophids (the intermediate hosts) and whales (the final hosts), which allow these parasites to cross the Polar Front (Klimpel et al. 2010). In Antarctic and sub-Antarctic waters, anisakid infections show a higher intensity than elsewhere, a fact that has been linked to an overall lower degree of habitat disturbance (Mattiucci & Nascetti 2007).

2.2.2. Kleptocommensal associations

Kleptocommensals represent a peculiar case of parasitism in which the 'symbionts' steal food accumulated by the host before this is ingested (Iyengar 2008). As 'true' parasites, they rely entirely on hosts for access to resources and, although there is not a direct damage of host tissues, they exert a detrimental effect on host fitness.

In Antarctica the family Capulidae (Caenogastropoda) numbers 9 species divided in the two genera *Capulus* Montfort, 1810 (1 species) and *Torellia* Jeffreys, 1867 (8 species), all kleptocommensals of sedentary polychaetes.

Of these species, the most widespread and common one is *Capulus subcompressus* Pelseneer, 1903 (Photo 1n), the unique capulid known from all the Antarctic continental margins (Map 14). The circumpolar distribution of this species, which invariably lives on the serpulid *Serpula narconensis* Baird, 1865 (Schiaparelli et al. 2000), seems to be assured by the existence of a peculiar larval structure (the "organic conch"), which enables long dispersal capabilities (Schiaparelli et al. 2000). In this association, symbiont's and host's distributions match quite well, although the host is also found in South America (Map 15).

For the genus *Torellia* few info about host preferences is known, possibly due to the fact that species belonging to this genus do exploit sessile polychaetes with pergamaceous and flexible tubes from which they are easily detached during sampling (Schiaparelli, unpublished).

Other kleptocommensals molluscs, such as *Waldo parasiticus* (Dall, 1876) (Photo 1o), live on irregular sea urchins of the genus *Abatus* Troschel, 1851 and probably take advantage of the food collected by the host, although detailed observations of these peculiarities are not available. *W. parasiticus*, which is widespread all around Antarctica, has a sister species known to occur only in South Georgia: *W. trapezialis* Zelaya & Ituarte, 2002.

3. Conclusions

On the whole, by examining all the information compiled in literature so far, there are clues that all but few of the known Antarctic marine partnerships may represent relict interactions already present on the continent before the isolation of Antarctica. At the present state of knowledge, this assumption is largely based on the fact that many of the above-described interactions are abundant outside Antarctica, where they encompass much larger spectra of species, both for hosts and symbionts, as well as a more widespread fossil occurrence (e.g. for epitoniids and cerithiopsids among Gastropoda).

However, several alternative hypotheses might be equally valid to explain the observed patterns and any generalisation is still premature. For example, some of the examples now considered as 'survivors' to cooling phases could simply have been reintroduced after a real extinction occurred, analogously to what happened in the case of the muricid genus *Trophonella* (Barco et al. 2012). On the other hand, the frequently documented cases of 'host-switch' or 'host-jump' (e.g. Schiaparelli et al. 2000, 2007, 2011b) tell us that, even for species living in association, survival in Antarctica during cooling and glacial cycles was possible, but the required price was a certain degree of ecological plasticity which lead to exploit new species/groups, different from the original ones.

At the present state of knowledge, only the association involving pycnogonids and the parasitic gastropod *Dickdellia* seems to have been truly established after the isolation of the Antarctic continent, when pycnogonids became a species-rich group with representatives of large size. This kind of interaction is, in fact, completely unknown outside Antarctica and could be

regarded as a truly Antarctic and endemic one.

In some other cases, such as that of the tanaid *Exspina typica* or the polynoid *Polyeunoa laevis*, which have both taxonomically and ecologically similar relatives in deep basins outside Antarctica, it is possible that Antarctica acted as a centre of radiation by exporting species through the thermohaline circulation, as occurred in other groups (Strugnell et al. 2008).

The always-growing body of genetic studies performed on Antarctic species is now revealing previously unnoticed complex patterns of colonisation and extinction events in several groups of organisms. Analogously to what happens for the species not living in association, the extant symbiotic associations may simply be a mix of the above-cited situations. Given the strict ecology of most symbionts, which are adapted to live in association to one species, genus or clade of hosts, studying their phylogenies and dispersal routes may be of great help in assessing the evolutionary history and duration of a 'symbiotic' relationship.

It will be of extreme importance to perform genetic studies on the partners of these symbiotic interactions in order to clarify their origin, their distributional patterns and their degree of genetic diversity, hopefully giving response to the several questions still unanswered.

Acknowledgements

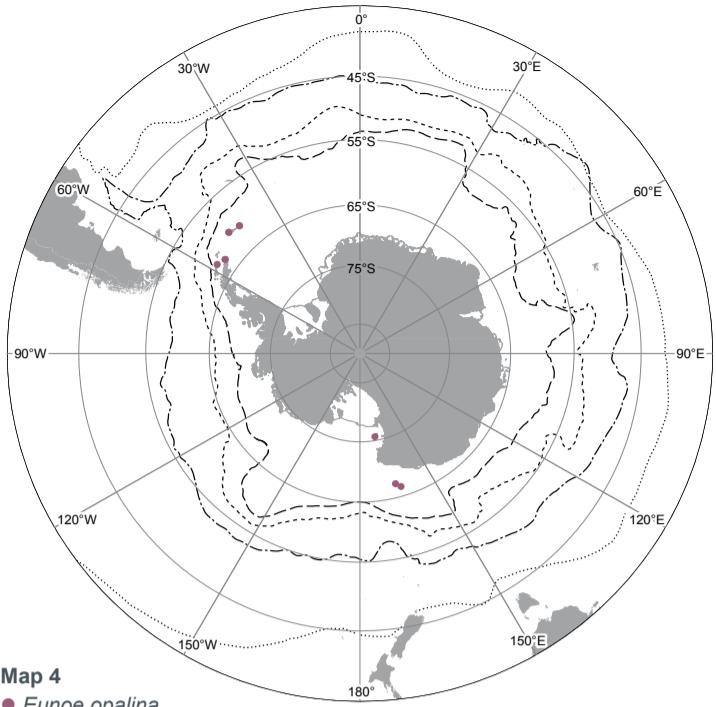
Photo 1l was taken in 2004 during the TAN0402 BIOROSS biodiversity survey of the western Ross Sea and Balleny Islands, undertaken by NIWA (National Institute of Water & Atmospheric Research) and financed by the former New Zealand Ministry of Fisheries. Pictures 1 a, 1b, 1e, 1f, 1h were taken during the TAN0802 IPY CAML expedition funded by the New Zealand Government under the New Zealand International Polar Year Census of Antarctic Marine Life Project (Phase 1: So001IPY; Phase 2; IPY2007-01). We gratefully acknowledge project governance provided by the Ministry of Fisheries Science Team and the Ocean Survey 20/20 CAML Advisory Group (Land Information New Zealand, Ministry of Fisheries, Antarctica New Zealand, Ministry of Foreign Affairs and Trade, and NIWA). Mario Santoro (Department of Public Health and Infectious Diseases, Sapienza, University of Rome) kindly provided literature references for Digenea, Cestoda, Nematoda and Acanthocephala and the picture in Photo 1n. Cédric d'Udekem d'Acoz (Royal Belgian Institute of Natural Sciences) kindly pointed out and gave information about the undescribed association between the lysianassoid *Adeliella* and an unknown holothuroid from the Larsen B area. Dr. Julian Gutt (AWI) and Dr. Marco Oliverio (University "La Sapienza", Rome) are acknowledged for their comments and suggestions, which greatly improved the MS. I'm indebted to Dr. Chiara Alvaro for her invaluable help during the writing of this MS, and to Dr Huw Griffiths (BAS, Cambridge) and Dr Anton Van de Putte (RBINS, Brussels) for the preparation of the maps. This is CAML contribution # 129 and BAMBi (Project PNRA 2010/A1.10, "Barcode of Antarctic Marine Biodiversity" contribution # 2.

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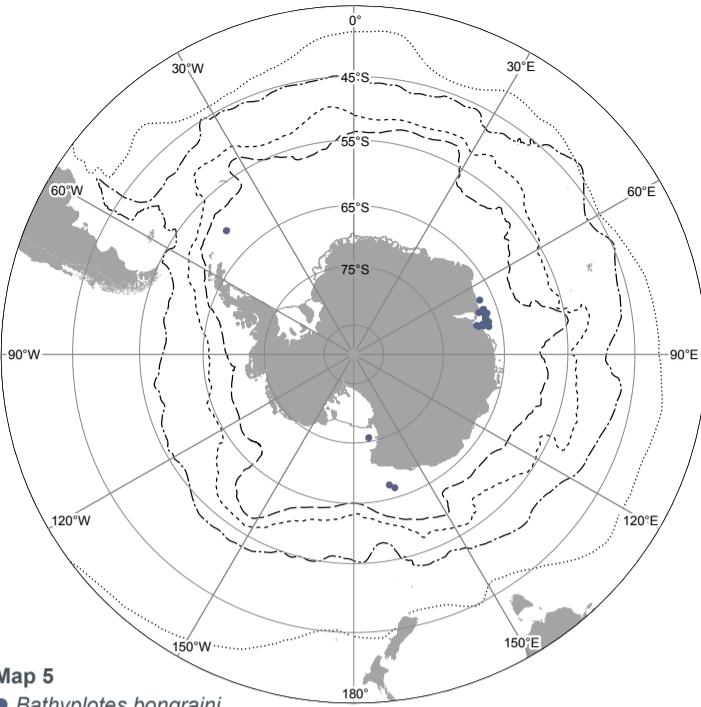
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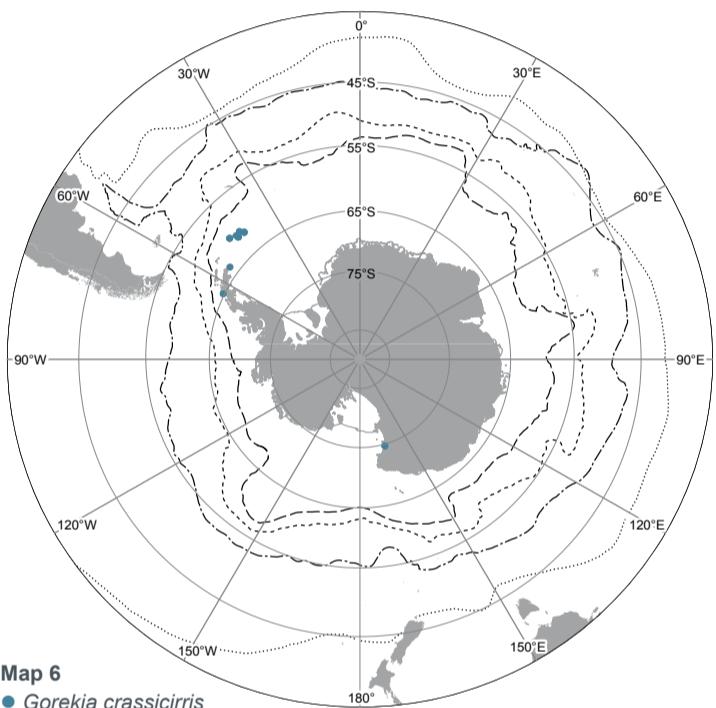
► Biotic Interactions



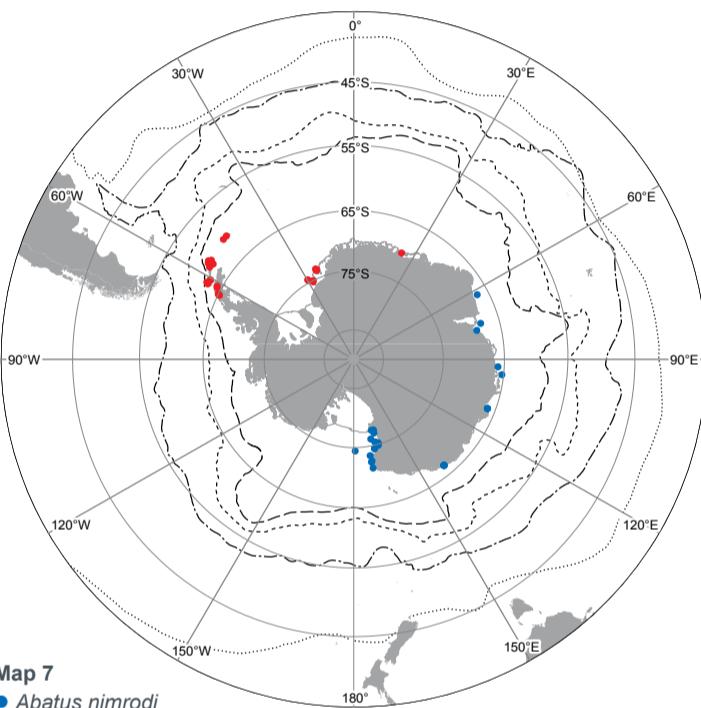
Map 4
● *Eunoe opalina*



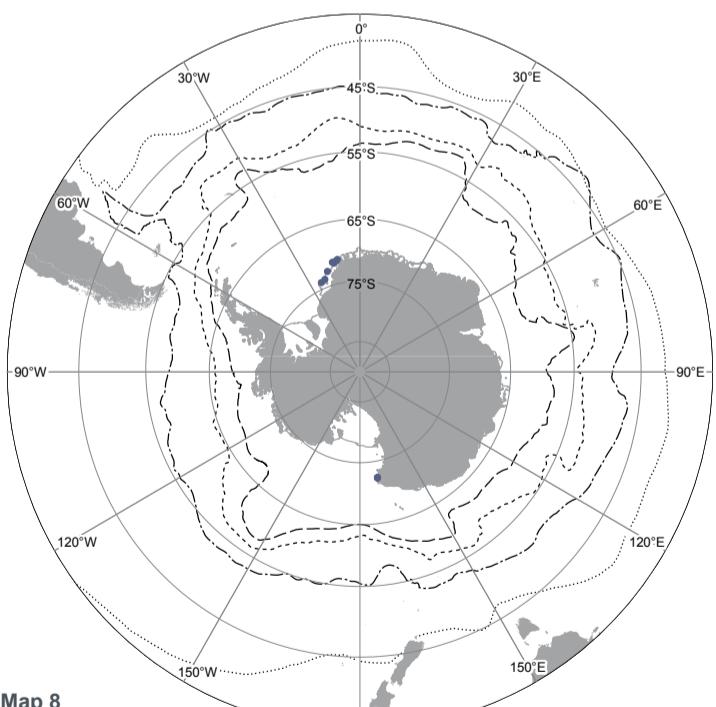
Map 5
● *Bathyploites bongraini*



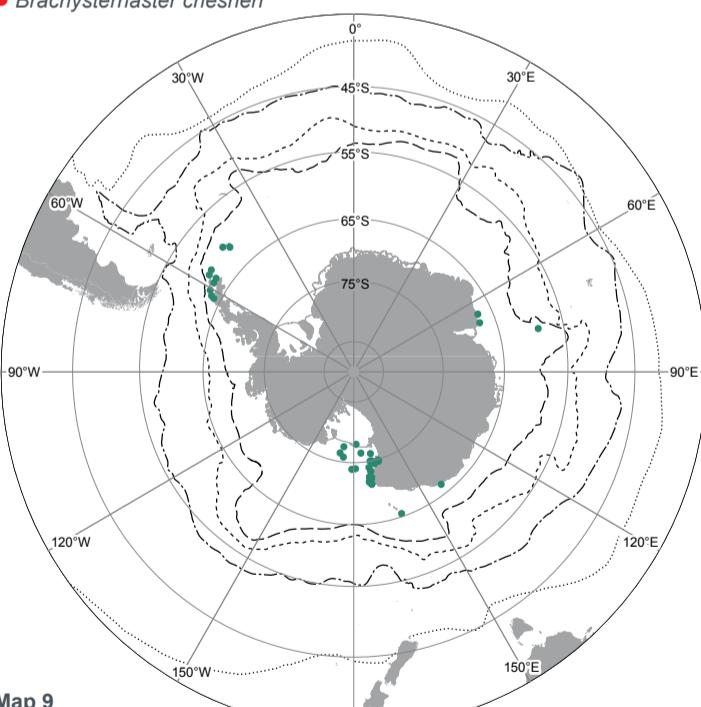
Map 6
● *Gorekia crassicirrhis*



Map 7
● *Abatus nimrodi*
● *Brachysternaster chesheri*

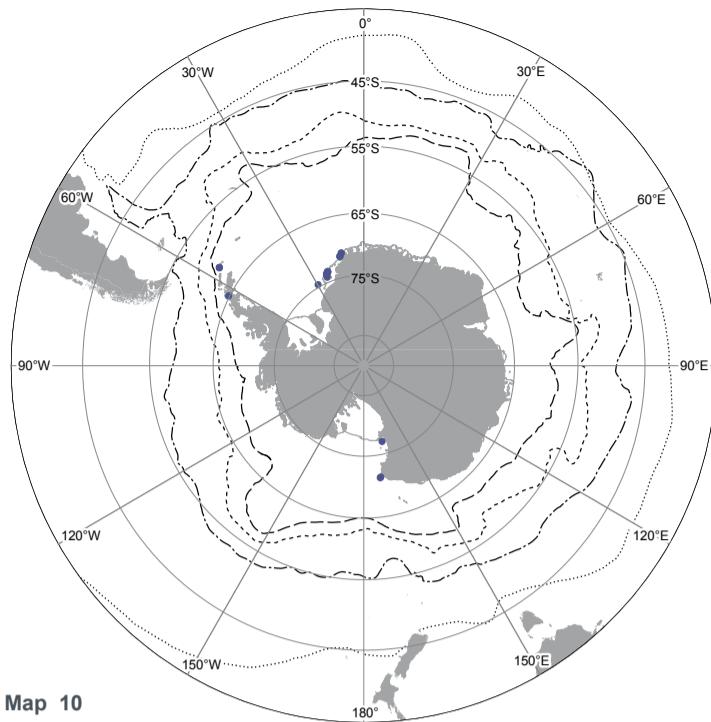


Map 8
● *Bathycrinicola tumidula*

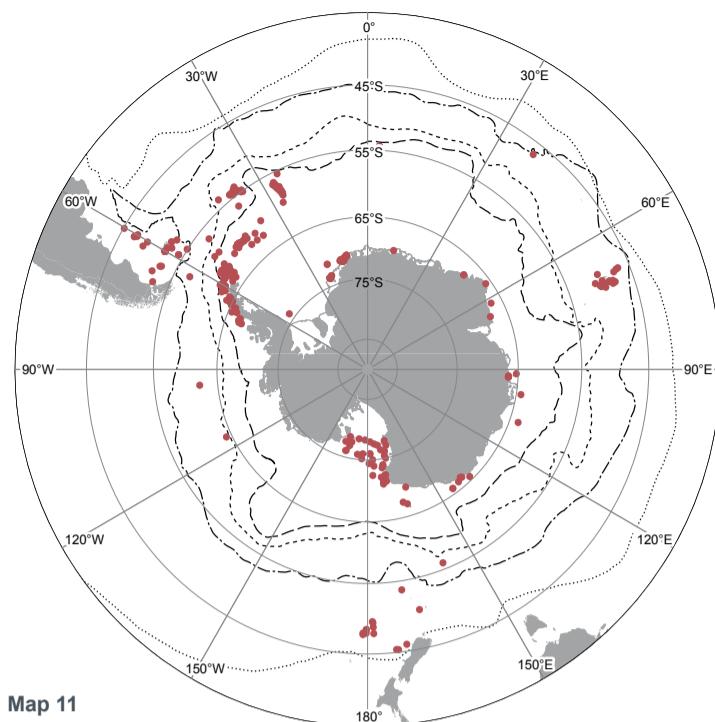


Map 9
● *Notocrinus virilis*

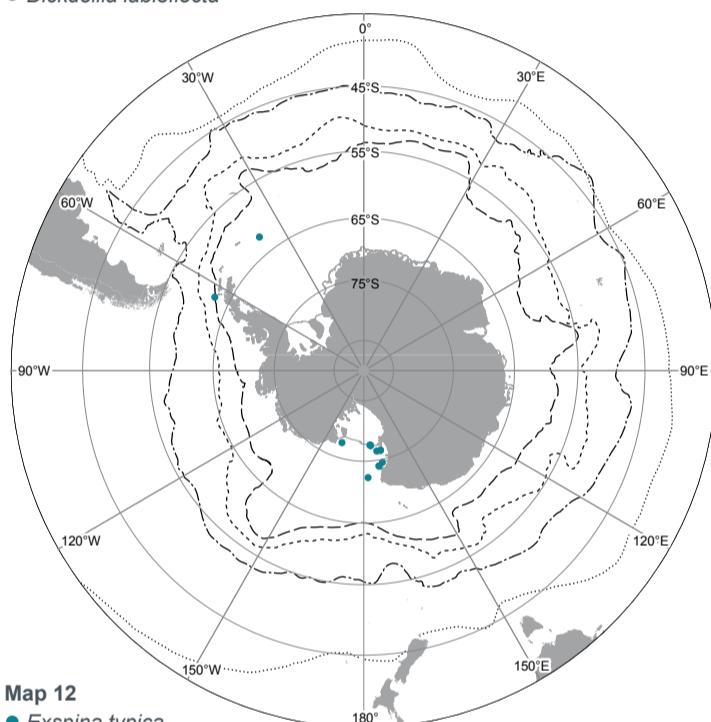
Biotic Interactions Maps 4–9 Map 4. Distribution of the polynoid *Eunoe opalina* McIntosh, 1885 (Photo 1f), which lives associated to the holothuroid *Bathyploites bongraini* (Map 5), based on SCAR-MarBIN data updated with data from Schiaparelli et al. (2010) for the Ross Sea. Map 5. Distribution of the holothuroid *Bathyploites bongraini* Vaney, 1914, host of the polynoid *Eunoe opalina*, based on SCAR-MarBIN data updated with data from Schiaparelli et al. (2010) for the Ross Sea. Map 6. Distribution of the polynoid *Gorekia crassicirrhis* (Willey, 1902) (Photo 1g), based on SCAR-MarBIN data and data from Schiaparelli et al. (2011); this polynoid is associated to two different hosts, which markedly differ in distribution (Map 7); also in this case no genetic data are available for the symbiont and the degree of divergence between the Ross Sea and the Antarctic Peninsula plus Scotia Arc islands is unknown. Map 7. Distribution of the two known hosts of the polynoid *Gorekia crassicirrhis*: the irregular sea urchin *Abatus* (*Pseudabatus*) *nimrodi* (Koehler, 1911) and *Brachysternaster chesheri* Larvain, 1985; the distribution of the two hosts should mirror that of the polynoid, at least at the potential level; *G. crassicirrhis* however has been signalled in fewer stations (see text and Schiaparelli et al. 2011b). Map 8. Distributional records of the parasitic eulimid *Bathycrinicola tumidula* (Thiele, 1912) (Photo 1h) from SCAR-MarBIN data plus the new records from the Ross Sea published in Schiaparelli et al. (2007); this species has been found so far only on the comatulid *Notocrinus virilis*. Map 9. Distributional records of the crinoid *Notocrinus virilis* Mortensen, 1917, host of *Bathycrinicola tumidula*; this distribution shows the host potential availability for the eulimid in Antarctic waters, although *B. tumidula* is seldom reported (see text for details).



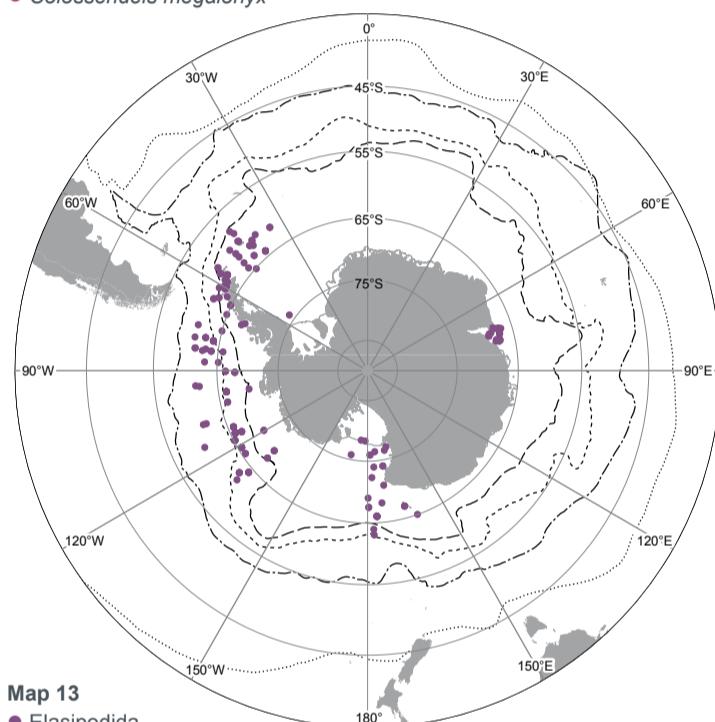
Map 10
● *Dickdellia labioflecta*



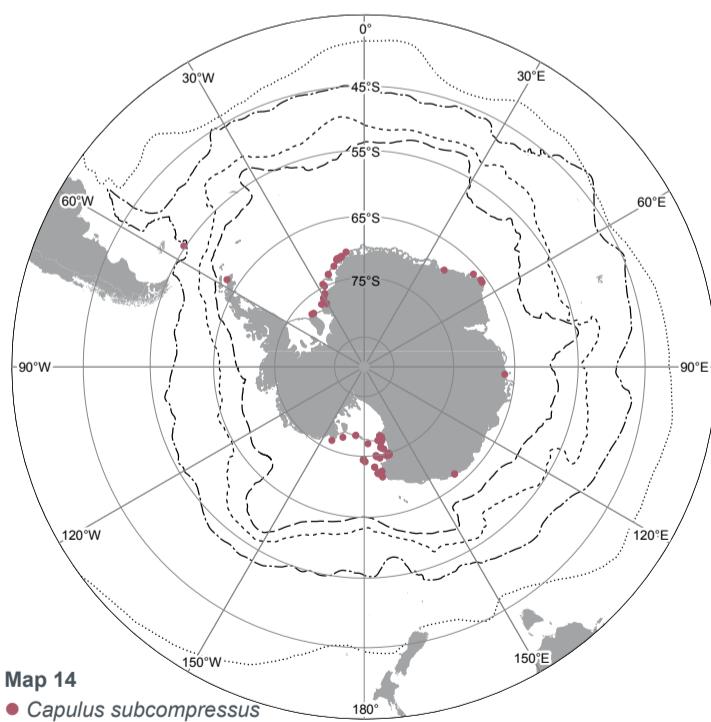
Map 11
● *Colossendeis megalonyx*



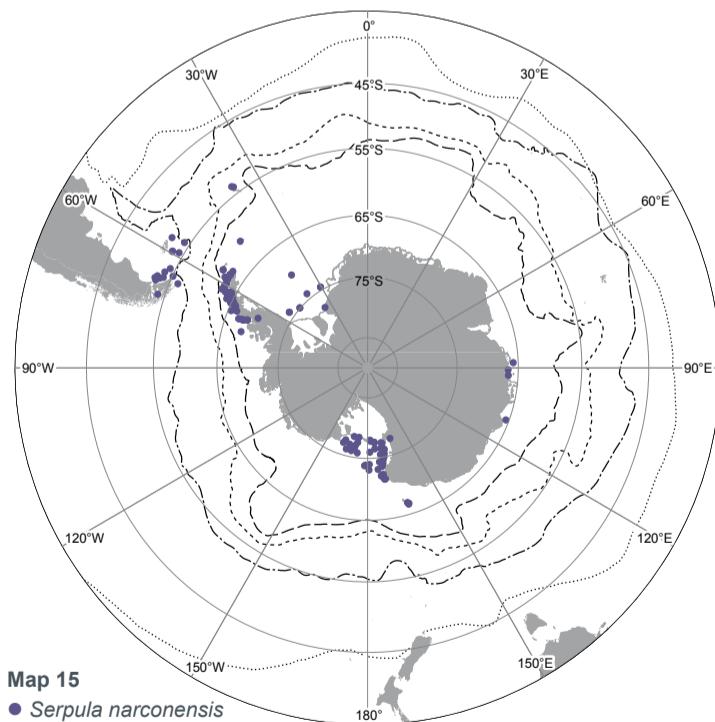
Map 12
● *Exspina typica*



Map 13
● *Elasipodida*



Map 14
● *Capulus subcompressus*



Map 15
● *Serpula narconensis*

Biotic Interactions Maps 10–15 Map 10. Known distribution of the zerotulid *Dickdellia labioflecta* (Dell, 1990) (Photo 1j), an Antarctic endemic species, which parasitizes several species of pycnogonids. Map 11. Distribution of one of the most common host of *Dickdellia labioflecta*, the pycnogonid *Colossendeis megalonyx* Hoek, 1881; the host distribution could mirror the potential host availability (and hence distribution) for the parasite; however, this apparently widespread species of pycnogonid is known to be formed by a mosaic of cryptic species and no genetic data exist for *D. labioflecta* to assess coherence in association between clades of the two species (see text for details). Map 12. Distribution of the parasitic tanaid *Exspina typica* Lang, 1968, which can be found inside the body of deep-water holothuroids belonging to Elasipodida; the few known records for Antarctic waters could dramatically increase if more elasipodids will be examined also through the study of ROV images (see text for details). Map 13. Known occurrence of all Elasipodida species from Antarctic waters, which mirrors the potential host availability for the parasitic tanaid *Exspina typica*. Map 14. Distribution of the kleptoparasitic gastropod *Capulus subcompressus*, Pelseneer, 1903 (Photo 1n), which lives on the serpulid *Serpula narconensis*, Baird, 1865. Map 15. Distribution of the host of *C. subcompressus*, the serpulid *Serpula narconensis* Baird, 1865, which is broadly consistent with that of *C. subcompressus*; *S. narconensis* can also be found in South America, although here it has never been reported in association with any gastropod species.

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THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

Scope

Biogeographic information is of fundamental importance for discovering marine biodiversity hotspots, detecting and understanding impacts of environmental changes, predicting future distributions, monitoring biodiversity, or supporting conservation and sustainable management strategies.

The recent extensive exploration and assessment of biodiversity by the Census of Antarctic Marine Life (CAML), and the intense compilation and validation efforts of Southern Ocean biogeographic data by the SCAR Marine Biodiversity Information Network (SCAR-MarBIN / OBIS) provided a unique opportunity to assess and synthesise the current knowledge on Southern Ocean biogeography.

The scope of the Biogeographic Atlas of the Southern Ocean is to present a concise synopsis of the present state of knowledge of the distributional patterns of the major benthic and pelagic taxa and of the key communities, in the light of biotic and abiotic factors operating within an evolutionary framework. Each chapter has been written by the most pertinent experts in their field, relying on vastly improved occurrence datasets from recent decades, as well as on new insights provided by molecular and phylogeographic approaches, and new methods of analysis, visualisation, modelling and prediction of biogeographic distributions.

A dynamic online version of the Biogeographic Atlas will be hosted on www.biodiversity.aq.

The Census of Antarctic Marine Life (CAML)

CAML (www.caml.aq) was a 5-year project that aimed at assessing the nature, distribution and abundance of all living organisms of the Southern Ocean. In this time of environmental change, CAML provided a comprehensive baseline information on the Antarctic marine biodiversity as a sound benchmark against which future change can reliably be assessed. CAML was initiated in 2005 as the regional Antarctic project of the worldwide programme Census of Marine Life (2000-2010) and was the most important biology project of the International Polar Year 2007-2009.

The SCAR Marine Biodiversity Information Network (SCAR-MarBIN)

In close connection with CAML, SCAR-MarBIN (www.scarmarbin.be, integrated into www.biodiversity.aq) compiled and managed the historic, current and new information (i.a. generated by CAML) on Antarctic marine biodiversity by establishing and supporting a distributed system of interoperable databases, forming the Antarctic regional node of the Ocean Biogeographic Information System (OBIS, www.iobis.org), under the aegis of SCAR (Scientific Committee on Antarctic Research, www.scar.org). SCAR-MarBIN established a comprehensive register of Antarctic marine species and, with biodiversity.aq provided free access to more than 2.9 million Antarctic georeferenced biodiversity data, which allowed more than 60 million downloads.

The Editorial Team



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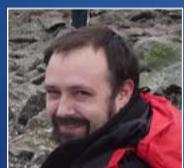
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