Polynoid polychaetes living in the gut of irregular sea urchins: a first case of inquilinism in the Southern Ocean

STEFANO SCHIAPARELLI¹, MARIA CHIARA ALVARO² and RUTH BARNICH³

¹Dipartimento per lo Studio del Territorio e delle sue Risorse (Dip.Te.Ris.), Università di Genova, C.so Europa 26, Genova I-16132, Italy

²Museo Nazionale dell'Antartide (MNA), Università di Genova, Viale Benedetto XV no. 5, Genova I-16132, Italy ³Forschungsinstitut Senckenberg, Senckenberganlage 25, D-60325 Frankfurt, Germany stefano.schiaparelli@unige.it

Abstract: Many different polychaete-echinoderm relationships have been described, from tropical to polar environments. Most of these associations have been generally defined as 'commensal', with polychaetes guests usually found on the oral surface of their hosts or, in a very few cases, even inside the host's body. Here we present an inquilinistic association involving two Antarctic species, the polychaete *Gorekia crassicirris* (Willey, 1902) (Polynoidae) and the irregular sea urchin *Abatus nimrodi* (Koheler, 1911) (Schizasteridae) found in the Ross Sea. This record is only the second worldwide for this kind of association, after that of the polychaete *Benthoscolex cubanus* which lives in the gut of the spatangoid *Archeopneustes hystrix* in Caribbean waters. *Gorekia crassicirris* seems to be a polyxenous species as it was also observed on another schizasterid, *Brachysternaster chescheri* Larrain, 1985 in the Weddell Sea. Considering that *A. nimrodi* is absent from that area and that the two sea urchin species have a disjoint distribution, it is possible that a 'host-switch' phenomenon occurred at some stage. We review the available literature to compare the Antarctic pairing with the other known examples of similar associations.

Received 9 September 2010, accepted 26 November 2010, first published online 1 February 2011

Key words: Antarctica, Echinoidea, Polychaeta, Ross Sea

Introduction

Polychaetous annelids are probably the most frequently encountered and abundant macrobenthic metazoans in marine environments and the establishment of close associations with other invertebrates is a rather common phenomenon for this group (Martin & Britayev 1998). Most of the known relationships regarding 'symbiotic' (*sensu* De Bary 1878) polychaetes have been generally considered as commensalism. However, these characterizations mostly rely only on an apparent lack of 'parasitic' features, rather than on direct evidence (Martin & Britayev 1998), with the exception of a very few cases where the parasitic relationship has been effectively demonstrated (e.g. Emson *et al.* 1993, Freeman *et al.* 1998, Britayev & Lyskin 2002, Schiaparelli *et al.* 2010).

'Symbiotic' polychaetes are usually associated with hosts that provide good shelter (e.g. burrowing animals), have advantageous protective morphological features (e.g. grooves) or have chemical defences, all peculiarities easily found among echinoderms, with examples among all five classes of this phylum (Martin & Britayev 1998). The numerous species of polychaetes associated with sea stars, sea urchins and brittle stars (mainly polynoids, but also hesionids and syllids) prefer the more protective oral surface of their hosts (Martin & Britayev 1998). In very few cases only, however, some polychaetes may also be found inside the host's body, either in its coelomic cavity (Monticelli 1892) or in the intestine (Emson *et al.* 1993). To date, the best described association of this kind is that of the polychaete *Benthoscolex cubanus* Hartman, 1942 (Fam. Amphinomidae), which has been found inside the gut of the irregular sea urchin *Archeopneustes hystrix* (A. Agassiz, 1880) (Fam. Asterostomatidae) in deep waters off the Bahamas (Emson *et al.* 1993). From this position, the polychaete is able to steal forams and other organic material from the host gut content and can move along the entire length of its host's digestive track, exiting through the anus (Emson *et al.* 1993).

Although it was clear that the polychaete removed food from the gut of the host, no negative effects on the sea urchin were observed (Emson *et al.* 1993). For this reason, Emson *et al.* (1993) defined *B. cubanus* as either a parasite or a commensal of *A. hystrix*.

In this paper we describe a similar case in Antarctica, representing the first record, for the Southern Ocean, of an inquilinistic relationships of this kind. Inquilinism is a particular kind of commensalism in which one organism lives within another, usually in some part of the alimentary tract or respiratory chamber, without being parasitic on it or causing it any serious harm (Dales 1957). This newly reported Antarctic case seems to fit this definition well. The partners of this Antarctic association are two known species, the irregular sea urchin *Abatus nimrodi* (Koehler, 1911) (Fam. Schizasteridae) and the polychaete *Gorekia crassicirris*

 Table I. List of sampling stations and of examined material. Complete specimens, used for size range measurements, are indicated by 'cs', while 'af' refers to anterior fragments. 'MM' refers to the mini movie available as supplementary material at www.journals.cambridge.org/jid_ANS.

 Species (Museum voucher)
 Host
 Expedition
 Date
 Station
 Depth
 Lat S
 Long E
 Remarks

 G. crassicirris (SMF 19451)
 A. nimrodi
 PNRA XXI
 27/01/2006
 BTN-DR 1
 90–145
 74°43.097
 164°08.860
 cs; Fig. 2

 G. crassicirris (SME 10450)
 A. nimrodi
 PNRA XXI
 27/01/2006
 BTN-DR 1
 90–145
 74°43.097
 164°08.860
 cs; Fig. 2

| C | 4 . 7. | DND A XXXI | 27/01/2006 | DTM DD 1 | 00 145 | 74942.007 | 1 < 490.0 0 < 0 | E. 0 |
|-----------------------------|-------------|------------|------------|----------|---------|-----------|-----------------|------------|
| G. crassicirris (SMF 19451) | A. nimrodi | PNRA XXI | 27/01/2006 | BTN-DR 1 | 90–145 | 74°43.097 | 164°08.860 | cs; Fig. 2 |
| G. crassicirris (SMF 19452) | A. nimrodi | PNRA XXI | 27/01/2006 | BTN-DR 1 | 90–145 | 74°43.097 | 164°08.860 | cs |
| G. crassicirris (MNA 2690) | A. nimrodi | PNRA XXI | 27/01/2006 | BTN-DR 1 | 90-145 | 74°43.097 | 164°08.860 | cs |
| G. crassicirris (MNA 2691) | A. nimrodi | PNRA XXI | 27/01/2006 | BTN-DR 1 | 90-145 | 74°43.097 | 164°08.860 | af |
| G. crassicirris (MNA 2692) | A. nimrodi | PNRA XXI | 27/01/2006 | BTN-DR 1 | 90-145 | 74°43.097 | 164°08.860 | af |
| G. crassicirris (MNA 2693) | A. nimrodi | PNRA XXI | 27/01/2006 | BTN-DR 1 | 90-145 | 74°43.097 | 164°08.860 | cs |
| G. crassicirris (MNA 2694) | A. nimrodi | PNRA XXI | 27/01/2006 | BTN-DR 1 | 90-145 | 74°43.097 | 164°08.860 | cs |
| G. crassicirris (MNA 2695) | A. nimrodi | PNRA XXI | 27/01/2006 | BTN-DR 1 | 90-145 | 74°43.097 | 164°08.860 | af |
| G. crassicirris (MNA 2696) | A. nimrodi | PNRA XVII | 17/01/2002 | DR 2 | 100-140 | 74°43.28 | 164°08.07 | cs (MM) |
| G. crassicirris (MNA 2697) | A. nimrodi | PNRA XXV | 05/12/2010 | DR 2 | 90-148 | 74°42.049 | 164°08.257 | |
| G. crassicirris (SMF 15269) | B. chesheri | ANT XV/3 | 04/02/1998 | 48-088 | 1353 | 73°29.0 | 22°35.2 | cs |

Abbreviations: PNRA = Programma Nazionale di Ricerca in Antartide (Italian National Antarctic Research Program), ANT = ANTARKTIS/3 (EASIZ II) of RV *Polarstern* in 1998, BTN = Baia Terra Nova (Terra Nova Bay), DR = Naturalist dredge.

(Willey, 1902) (Fam. Polynoidae). This scaleworm has been reported, so far, only as a free-living species on incoherent substrates of all grain sizes (Hartmann-Schröder & Rosenfeldt 1988) and has a circumpolar distribution, being present around the Antarctic Peninsula, in the South Orkney Islands and in the Ross Sea, from 37–2012 m (Stiller 1996, Knox & Cameron 1998). Analogously, the deposit feeding sea urchin has a circumpolar distribution occurring in the Ross, Dumont d'Urville and Davis seas, from 13–732 m. (David *et al.* 2003), where it has been observed more or less buried in a silty/sandy sediment (Chenuil *et al.* 2004).

In the light of the present finding we have reviewed the available literature regarding associations between polychaetes (even families different from Polynoidae) and echinoderms and examined the similarities/differences with the other known examples from outside Antarctic waters.

Material and methods

Most of the material examined was collected in the Ross Sea, at Terra Nova Bay, in the course of three different PNRA (Italian National Antarctic Research Program) expeditions (XVII, XXI, and XXV) carried out from 2001 to 2010. The specimens of *G. crassicirris* associated with *A. nimrodi* studied here were sampled by means of a naturalist dredge at different coastal stations on detritic bottoms (from 90–148 m) in front of the Mario Zucchelli Station (Table I). *In vivo* behavioural observations of *G. crassicirris* on *A. nimrodi* were performed and recorded (pictures and mini movies) with a digital camera (Nikon Coolpix 4500) before fixation in 80% ethanol.

The diagnostic characters of the polychaetes were studied using a stereomicroscope equipped with a camera lucida apparatus and a Normaski interference contrast compound microscope. Morphometric measures were taken as follows: length (L), taken from the anterior margin of the prostomium to the posterior border of the last segment (pharynx not included, if extended); width (W), taken at approximately the largest segment, including parapodia but excluding chaetae. An attempt to analyse the stomach content of some specimens of *G. crassicirris* was made in order to characterize the food spectrum of the polychaete as in Schiaparelli *et al.* (2010), but no food was found inside the gut of the three examined specimens. In order not to damage all the available material, no further dissections were performed.

Host specimens were identified by using the dichothomous keys from the 'Antarctic Echinoids interactive database' (David *et al.* 2003).

According to the available literature, other examples of associations involving polychaetes and echinoderms have been considered, but taking only into account guests and hosts that were identified at least at a genus level. Moreover, we focused only on those partnerships in which the associated polychaete was found along the oral side of the host, more or less close to its mouth, if not directly inside the gut or body cavity (see Supplementary Table I at www.journals.cambridge.org/ jid ANS for further details and bibliographic references). Examples in which the polychaete was generically reported as 'on the host surface' or 'on aboral side' were not considered. in order to exclude possible occasional epibiotic association. For polyxenous polychaetes, i.e. a single polychaete species associated with several hosts belonging to one/two distinct echinoderm classes (e.g. Arctonoe pulchra Johnson, 1897), each literature record was considered separately for calculations. The same was done for hosts with two (or more) different species of polychaetes (e.g. Ophiodromus flexuosus (Delle Chiaje, 1825) and Acholoe astericola (Delle Chiaje, 1841), both observed on Astropecten irregularis (Pennant, 1777)). Gastrolepidia clavigera Schmarda, 1861 represents another exception, being reported by Britayev & Zamishliak (1996) as entering both oral and cloacal cavities of its hosts, but without a specific indication of which species, among the 11 possible different hosts, it is the subject of this behaviour. In this case, we preferred to consider these potentially multiple examples as a single record.

Taxonomic names were checked following WoRMS (World Register of Marine Species, www.marinespecies.org; last search 7 May 2010). Voucher material is deposited at

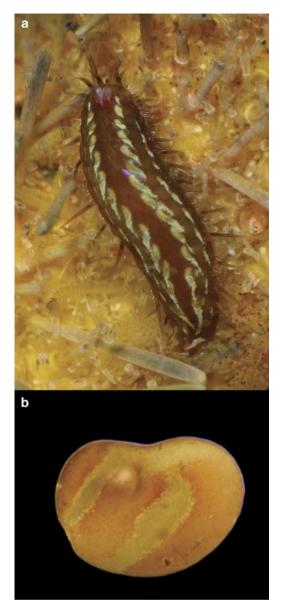


Fig. 1. The scale worm *Gorekia crassicirris* on its host, the irregular sea urchin *Abatus nimrodi*. **a.** Specimen of *G. crassicirris*, dorsal view. **b.** Elytron of *G. crassicirris* showing the typical colour pattern with two lighter bands.

the Italian National Antarctic Museum (MNA) and at the Senckenberg Museum Frankfurt (SMF) (Table I).

Results

A 'symbiotic' relationship involving the Antarctic scaleworm *G. crassicirris* (Fig. 1) and the irregular sea urchin *A. nimrodi* is here described.

Systematic part

Family Polynoidae Kinberg, 1856 Genus *Gorekia* Bergström, 1916

Type species. Malmgrenia crassicirris Willey, 1902.

Diagnosis. Body flattened dorsoventrally, short, up to 38 segments, more or less covered by elytra. Elytra 15 pairs on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23, 26, 29, 32. Prostomium bilobed, without cephalic peaks, with three antennae; lateral antennae with ceratophores inserted terminoventrally to median antenna; two pairs of eyes, anterior pair dorsolateral at widest part of prostomium, posterior pair dorsal near hind margin of prostomium. Parapodia biramous, noto- and neuropodia with elongate acicular lobe; tips of noto- and neuropodia with elongate stouter than neurochaetae, with rows of spines and blunt or notched tips; neurochaetae more numerous, with rows of spines only distally and tridentate tips.

Gorekia crassicirris (Willey, 1902) (Figs 1 & 2)

Malmgrenia crassicirris Willey, 1902: 269, pl. 42 figs 3 & 4, pl. 44 figs 5 & 6.

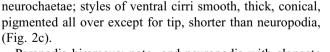
Gorekia crassicirris: Bergström (1916): 295, pl. 3 fig. 9, pl. 5 figs 3–6; Uschakov (1962): 170, pl. 8 figs F–J; Hartman (1964): 23, pl. 6 figs 4 & 5; Hartmann-Schröder & Rosenfeldt (1988): 29; Stiller (1996): 35, pl. 15; Knox & Cameron (1998): 27 figs 47–50.

Measurements. Specimen figured (SMF 19451: L 10 mm, W 2.5 mm for 37 segments). Size range for seven complete specimens investigated herein: L 6–13 mm, W 2–3.5 mm for 27–38 segments.

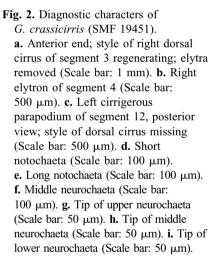
Description

Prostomium bilobed, without cephalic peaks; median antenna with ceratophore in anterior notch, style smooth, tapering, with pigmented bands basally and subdistally; lateral antennae with ceratophores inserted terminoventrally and with short, smooth, tapering styles with pigmented band subdistally; palps smooth, stout, tapering; anterior pair of eyes dorsolaterally at widest part of prostomium, posterior pair dorsally near hind margin, but rather close to anterior pair (Fig. 2a). Tentaculophores inserted laterally to prostomium, without chaetae on inner side, but with a pair of smooth, tapering dorsal and ventral tentacular cirri; styles of tentacular cirri usually distinctly pigmented basally and subdistally (Fig. 2a). Second segment with first pair of elytra, biramous parapodia, and long ventral buccal cirri, similar to tentacular cirri.

Fifteen pairs of elytra; elytral surface and margin smooth, without papillae or tubercles, surface more or less pigmented (brownish in ethanol, reddish in life), with two unpigmented stripes diagonally (white in life) (Fig. 2b). Styles of dorsal cirri smooth, tapering, with pigmented bands basally and subdistally, extending beyond tips of



Parapodia biramous; noto- and neuropodia with elongate acicular lobe; tips of noto- and neuroacicula penetrating epidermis; neuropodia with thick, digitiform supra-acicular process (Fig. 2c). Short and long notochaetae stout with blunt or notched tips and faint rows of spines (Fig. 2d & e). Neurochaetae with rows of spines only in distal part, uppermost rows with very strong spines; tips of neurochaetae tridentate with smaller tertiary tooth between main and secondary tooth; in lower neurochaetae tertiary tooth often minute, less distinct than in upper and middle neurochaetae (Fig. 2 f–i).

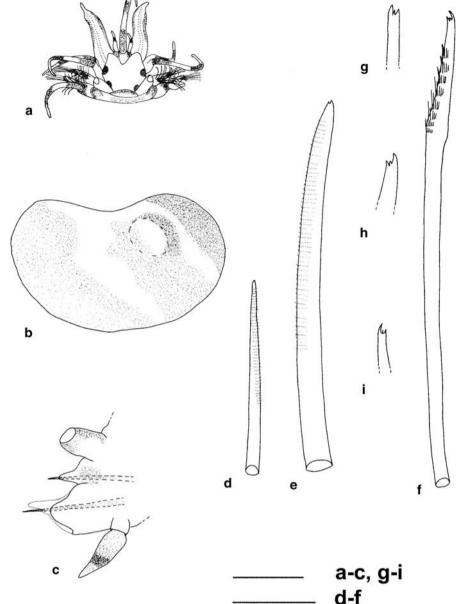


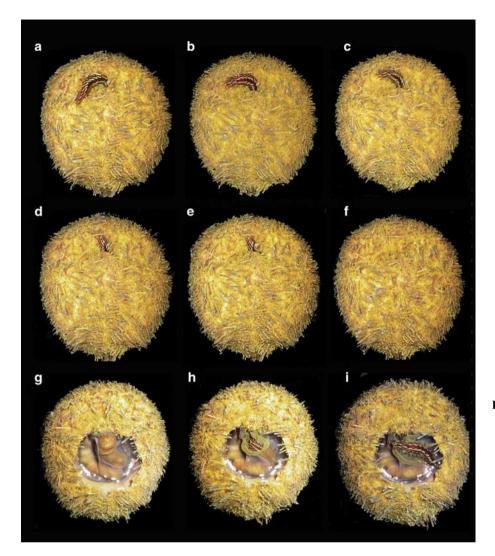
Type species. Spatangus (Tripylus) cavernosus Philippi, 1845, p. 435, by original designation.

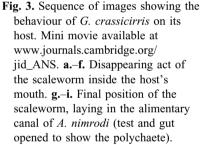
Family Schizasteridae Lambert, 1905 Genus *Abatus* Troschel, 1851

Description (from David et al. 2003)

Test of variable ambital outline, rounded without any trace of frontal notch in species such as *A. nimrodi*, or conspicuously but not deeply indented such as in *A. cavernosus* or *A. cordatus*. Apical system subcentral with three genital pores. Paired petals deeply sunken into marsupia in females, and flushed with the test in males. The genus *Abatus* is characterized by the presence of a "peripetalous" fasciole







in adults. All types of pedicellarie present, except the ophicephalous form.

Abatus nimrodi (Koehler, 1911)

Pseudabatus nimrodi Koehler, 1911: 60, pl. 7 figs 1-8, pl. 8 figs 7-12

Pseudabatus nimrodi: Bell (1917): 3.

Abatus (Pseudabatus) nimrodi: Mortensen (1951): 263.

Abatus nimrodi, Lockhart et al. (1994): 754, figs 3 & 4.

Measurements. The average length of the test is generally about 30–40 mm, but can be to 60 mm.

Description (from David et al. 2003)

The main characteristic of *A. nimrodi* is that the depressed part of the petals is widely separated from the apical system. This feature is particularly conspicuous in females, in which

the brood pouches start as far as 7 or 9 ambulacral plates distant from the apical system. General outline of the ambitus rounded, without frontal notch, slightly attenutated posteriorly. Test flattened aborally. Periproct located on the short vertical posterior end, and scarcely visible in either aboral or oral views. Labrum large, extending to the 2nd or 4th adjacent ambulacral plates, but not distinctly overhanging the peristome. Valves of globiferous pedicellariae terminating in a series of small teeth. Bidentate pedicellariae very abundant all over the test. Colour of preserved specimens dark-brown to almost black.

Description of the association

Overall, seven complete specimens of *G. crassicirris* were measured, resulting in a range of length and width of 6–13 mm and 2–3.5 mm, respectively, for 27 to 38 segments. Of these polychaetes, four were obtained from undamaged sea urchins and the existence of a possible correlation between their length and the tests' major and minor diameter

was verified. No significative correlation was found but, as the number of investigated specimens is so small, this result has to be considered provisional. The infestation rate was evaluated during the XXI PNRA Expedition (2005-06) considering 14 individuals of A. nimrodi collected in a single catch. Eight of these had a polychaete in the gut, accounting for 57% of the total. In the remaining ones no traces of the polychaete could be observed either inside or outside the test. Most polychaetes were found to leave the host gut after few hours of maintenance in small aquaria ($T = 0-1^{\circ}C$), possibly due to oxygen depletion in the water. The crawling of the polychaetes on the host body did not provoke any reaction in the hosts, pedicellariae having been never observed to be used against the scaleworms. When sea urchins were placed upside down, in order to document the polychaetes' movements along the oral side of the host, the scaleworms were repeatedly observed actively searching the mouth opening and entering it (Fig. 1 and movie in supplementary material available at www.journals.cambridge.org/jid_ANS). Dissection of hosts, performed immediately after the polychaete disappearance inside the mouth, revealed that it laid oriented along the gut (Fig. 3g-i). If disturbed by tactile stimuli, the polychaete was able to turn quickly around within the gut, moving away from the stimulus.

Since *G. crassicirris* has been previously considered a free-living polychaete, occurring only in north-western Antarctica (Antarctic Peninsula and the South Orkney Islands) (Stiller 1996) and in several areas of the Ross Sea (Knox & Cameron 1998), the record herein reported represents the first for Terra Nova Bay, but also for this kind of association for the whole Southern Ocean. However, *G. crassicirris* is not associated exclusively with *A. nimrodi*, since it was also found together with *Brachysternaster chesheri* Larrain, 1985 in the south Vestkapp area (Weddell Sea), at 1353 m (*Polarstern* cruise ANT XV/3, 1998) (Barnich unpublished data).

Discussion

The establishment of a partnership with an echinoderm host can undoubtedly assure many advantages to a 'symbiont' (Davenport 1966). A calcareous test (e.g. sea urchins) or a tough skin sometimes covered with bumps (e.g. holothuroids), as well as pointed spines (e.g. sea urchins, sea stars), do not only reduce potential predation on the host, but also transfer this benefit to the guest as well (Davenport 1966), according to what is known as 'interspecific facilitation' (Bruno *et al.* 2003). Such a combination of surface morphological features and 'protective devices' makes echinoderms a particularly attractive niche for numerous organisms (e.g. Davenport 1966, Jangoux 1987a, 1987b), including polychaetous annelids.

Among polychaetous annelids, more than half (55%) of all species that are currently defined as commensal belong to Polynoidae (Martin & Britayev 1998) and many different

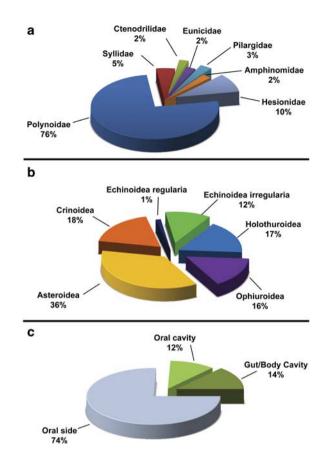


Fig. 4. Review of literature data. a. Taxonomic distribution of polychaete species involved in association with different echinoderm hosts. b. Allocation of polychaetes per host group (i.e. classes of echinoderms). c. Polychaete position on the host body. Information inferred from literature data, as specified in the Material and methods section. For full references and main features of the different polychaeteechinoderm associations considered see Supplemental Table I at www.journals.cambridge.org/jid_ANS.

polynoid-echinoderm associations have been described, from tropical to polar environments (Pettibone 1993, Freeman *et al.* 1998, Martin & Britayev 1998, Britayev & Lyskin 2002, Schiaparelli *et al.* 2010).

To review the available data, we took into account the best documented literature examples of polychaete (all families) and echinoderm (all classes) worldwide-distributed associations, focusing exclusively on those records of polychaetes that were found on the oral side of their echinoderm hosts, if not directly within its gut or body cavity, and attempted to highlight possible similarities with the Antarctic counterpart.

The pie charts in Fig. 4 summarize the information inferred from literature data (as specified in the Material and methods section). It is clear that most of the 'commensal' polychaete species (76%) belong to the family Polynoidae (Fig. 4a), while Asteroidea represents the most 'infested' class (37%) among Echinodermata (Fig. 4b). Furthermore, regardless of the polychaete family or the echinoderm class, in the majority (74%) of associations the polychaete guest is only found on the oral side of the host (Fig. 4c) although it does not seem to enter the oral cavity/gut with its anterior end.

Up to now, G. crassicirris is the only species, among Polynoidae, found to be able to completely enter the gut of a spatangoid, representing an 'exception' within the group. In fact, all other scaleworms just crawl partly into the stomach of their hosts and feed there, as the polynoid Acholoe astericola (Delle Chiaje, 1841) on the host Astropecten irregularis (Pennant, 1777) (Davenport 1953). Moreover, by considering the case of the amphinomid polychaete Benthoscolex cubanus, which is the only other known polychaete (not polynoid) that usually stays in the alimentary canal of an irregular sea urchin, our new Antarctic record represents the second worldwide example of such behaviour. Despite the very limited sample size available in our case, it is possible to highlight two similarities with B. cubanus (Emson et al. 1993), i.e. the lack of any relationships between the size of the associated worms and that of the hosts, and a similar infestation rate (57% in Abatus and 65% in Archeopneustes).

As already pointed out by Emson *et al.* (1993), irregular sea urchins might be regarded as preferable hosts, due to the fact that access to the gut does not involve 'negotiating' an Aristotle's lantern or ascending to the aboral anus. Curiously, in Antarctica, even if spatangoid sea urchins constitute 39% of the Southern Ocean echinoids (RAMS 2010), such a kind of association has never been recorded before but may be much more widespread, involving even other host species.

Unlike *B. cubanus*, *G. crassicirris* has been mainly observed in the initial portion of the host's gut and, at least in laboratory conditions, the polychaete has never been seen going through the alimentary canal to exit from the anus as it has been reported for the previous species (Emson *et al.* 1993).

The apparently empty stomachs of G. crassicirris prevented us from evaluating if its food spectrum somehow overlaps with that of the host and therefore whether the polychaete depends on the sea urchin for food. In the case of the amphinomid B. cubanus, this association has been defined as either commensal or parasitic (due to the stealing of food) by Emson et al. (1993). Further studies will be necessary to characterize better the Antarctic relationship. However, a possible interpretation of the 'symbiotic relationship' between G. crassicirris and A. nimrodi as an example of inquilinism can be suggested from previous works on polychaetes associated with holothuroids. Monticelli (1892) and Ganapati & Radhakrishna (1962), in fact, described similar associations in which polychaetes of several families (Syllidae, Ctenodrilidae and Hesionidae) have been found in the body cavity or in the intestine of holothuroid hosts. In both cases, authors defined those 'symbiotic relationships' as examples of inquilinism.

In the light of the behaviour observed during experimental conditions and considering the location of *G. crassicirris*,

inside the gut of A. nimrodi, we interpret such an association as a further example of inquilinism, although endoparasitism cannot be excluded since we have not been able to evaluate the possible damage caused by the polychaete to its host. For both B. cubanus and G. crassicirris, there seems to be a strict host-guest specificity: the Caribbean polychaete has been found only on a precise species of irregular sea urchin. The same situation has been recorded for G. crassicirris, which in the Ross Sea is associated only with A. nimrodi, even if two more species of Schizasteridae occur (also sympatrically) at Terra Nova Bay (A. elongatus (Koehler, 1908) and A. shackletoni Koehler, 1911) (Chiantore et al. 2006). On the other hand, G. crassicirris was also found in the Weddell Sea, on the peristomium of B. chescheri, another irregular sea urchin belonging to the same family (Schizasteridae) as A. nimrodi. Considering that the latter species is absent from that area (David et al. 2003), it could be argued that a host-switch phenomenon occurred at some stage, due to the disjoint distribution of the two sea urchin species, as already previously suggested in other cases of Antarctic invertebrates living in close association (e.g. Schiaparelli et al. 2000, 2007).

Acknowledgements

We thank the Italian National Antarctic Program (PNRA) for funding and logistic support. We are indebted to Dr Christian Neumann (Naturkundemuseum, Berlin) for bringing to our attention the record of *G. crassicirris* from the XV/3 *Polarstern* Expedition. Two anonymous reviewers are acknowledged for their useful comments on the manuscript. Hanny Rivera (Harvard College) kindly revised the English language. This is CAML contribution 55.

Supplemental material

A supplemental table and a mini movie will be found at www.journals.cambridge.org/jid_ANS.

References

- BERGSTRÖM, E. 1916. Die Polynoiden der schwedischen Südpolarexpedition 1901–1903. Zoologiska bidrag från Uppsala, 4, 269–304.
- BRITAYEV, T.A. & LYSKIN, S.A. 2002. Feeding of the symbiotic polychaete Gastrolepidia clavigera (Polynoidae) and its interactions with its hosts. Doklady Biological Sciences, 385, 352–356.
- BRITAYEV, T.A. & ZAMISHLIAK, E.A. 1996. Association of the commensal scaleworm *Gastrolepidia clavigera* (Polychaeta: Polynoidae) with holothurians near the coast of South Vietnam. *Ophelia*, **45**, 175–190.
- BRUNO, J.F., STACHOWICZ, J.J. & BERTNESS, M.D. 2003. Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution*, 18, 119–125.
- CHENUIL, A., GAULT, A. & FÉRAL, J.P. 2004. Paternity analysis in the Antarctic brooding sea urchin *Abatus nimrodi*: a pilot study. *Polar Biology*, **27**, 177–182.
- CHIANTORE, M., GUIDETTI, M., CAVALLERO, M., DE DOMENICO, F., ALBERTELLI, G. & CATTANEO-VIETTI, R. 2006. Sea urchins, sea stars and brittle stars from Terra Nova Bay (Ross Sea, Antarctica). *Polar Biology*, **29**, 467–475.

- DALES, R.P. 1957. Interrelations of organisms: A. Commensalism. Memoirs of the Geological Society of America, 67, 391–412.
- DAVENPORT, D. 1953. Studies in the physiology of commensalism. III. The polynoid genera *Acholoe, Gattyana* and *Lepidasthenia. Journal* of the Marine Biological Association of the United Kingdom, **32**, 161–173.
- DAVENPORT, D. 1966. Echinoderms and the control of behaviour in associations. *In* BOOLOOTIAN, R.A., *ed. Physiology of Echinodermata*. New York: Interscience, 145–156.
- DAVID, B., CHONE, T., DE RIDDER, C. & FESTAU, A. 2003. Antarctic echinoids: an interactive database. Version 2.0. Biogéosciences, University of Burgundy, CD-ROM.
- DE BARY, A.H. 1878. Über Symbiose. Tagblatt der 51. Versammlung Deutscher Naturforscher und Aerzte in Cassel. Kassel: Baier & Lewalter, 121–126.
- EMSON, R.H., YOUNG, C.M. & PATERSON, G.L.J. 1993. A fire worm with a sheltered life: studies of *Benthoscolex cubanus* Hartman (Amphinomidae), an internal associate of the bathyal sea urchin *Archeopneustes hystrix* (A. Agassiz, 1880). *Journal of Natural History*, 27, 1013–1028.
- FREEMAN, S.M., RICHARDSON, C.A. & SEED, R. 1998. The distribution and occurrence of *Acholoe squamosa* (Polychaeta: Polynoidae) a commensal with the burrowing starfish *Astropecten irregularis* (Echinodermata: Asteroidea). *Estuarine, Coastal and Shelf Science*, 47, 107–118.
- GANAPATI, P.N. & RADHAKRISHNA, Y. 1962. Inquilinism between a new hesionid and a holothurian *Molpadia* sp. *Current Science*, **31**, 382–383.
- HARTMAN, O. 1964. Polychaeta Errantia of Antarctica. Antarctic Research Series, 3, 1–131.
- HARTMANN-SCHRÖDER, G. & ROSENFELDT, P. 1988. Die Polychaeten der "Polarstern"-Reise ANT III/2 in die Antarktis 1984. Teil 1: Euphrosinidae bis Chaetopteridae. Mitteilungen des hamburgischen zoologischen Museums und Instituts, 85, 25–72.
- JANGOUX, M. 1987a. Diseases of Echinodermata. II. Agents metazoans (Mesozoa to Bryozoa). Diseases of Aquatic Organisms, 2, 205–234.
- JANGOUX, M. 1987b. Diseases of Echinodermata. III. Agents metazoans (Annelida to Pisces). Diseases of Aquatic Organisms, 3, 59–83.
- KNOX, G.A. & CAMERON, D.B. 1998. The marine fauna of the Ross Sea: Polychaeta. National Institute of Water and Atmospheric Research, Biodiversity Memoir, 108, 1–125.

- KROH, A. & HANSSON, H. 2010. Spatangoida. In KROH, A. & MOOI, R., eds. World Echinoidea Database. Accessed through: DE BROYER, C., CLARKE, A., KOUBBI, P.; PAKHOMOV, E., SCOTT, F., VAN DEN BERGHE, E. & DANIS, B., eds. The SCAR-MarBIN Register of Antarctic Marine Species (RAMS) at http://www.scarmarbin.be/rams.php?p=taxdetails&id=123106 accessed on 7 May 2010.
- MARTIN, D. & BRITAYEV, T.A. 1998. Symbiotic polychaetes: review of known species. Oceanography and Marine Biology Annual Review, 36, 217–340.
- MONTICELLI, F.S. 1892. Notizia preliminare intorno ad alcuni inquilini degli Holothuroidea del Golfo di Napoli. *Monitore Zoologico Italiano*, **3**, 248–256.
- PETTIBONE, M.H. 1993. Scaled polychaetes (Polynoidae) associated with ophiuroids and other invertebrates and review of species referred to *Malmgrenia* McIntosh and replaced by *Malmgreniella* Hartman, with descriptions of new taxa. *Smithsonian Contributions to Zoology*, **538**, 92 pp.
- SCHIAPARELLI, S., CATTANEO-VIETTI, R. & CHIANTORE, M. 2000. Adaptive morphology of *Capulus subcompressus* Pelseneer, 1903 (Gastropoda: Capulidae) from Terra Nova Bay, Ross Sea (Antarctica). *Polar Biology*, 23, 11–16.
- SCHIAPARELLI, S., ALVARO, M.C., BOHN, J. & ALBERTELLI, G. 2010. 'Hitchhiker' polynoid polychaetes in cold deep waters and their potential influence on benthic soft bottom food webs. *Antarctic Science*, **22**, 399–407.
- SCHIAPARELLI, S., GHIRARDO, C., BOHN, J., CHIANTORE, M., ALBERTELLI, G. & CATTANEO-VIETTI, R. 2007. Antarctic associations: the parasitic relationship between the gastropod *Bathycrinicola tumidula* (Thiele, 1912) (Ptenoglossa: Eulimidae) and the comatulid *Notocrinus virilis* Mortensen, 1917 (Crinoidea: Notocrinidae) in the Ross Sea. *Polar Biology*, **30**, 1545–1555.
- STILLER, M. 1996. Verbreitung und Lebensweise der Aphroditiden und Polynoiden (Polychaeta) im östlichen Weddellmeer und im Lazarevmeer (Antarktis). Berichte zur Polarforschung, 185, 1–200.
- USCHAKOV, P.V. 1962. Polychaetous annelids of the family Phyllodocidae and Aphroditidae from the Antarctic and Subantarctic (Material collected by the Soviet Antarctic Expedition, 1955–1958). *Studies of Marine Fauna. Biological Reports of the Soviet Antarctic Expedition* (1955–1958), **1**, 131–188 (translated 1966 by the Israel Program for Scientific Translations).
- WILLEY, A. 1902. Report on the collections of natural history made in Antarctic regions during the voyage of the "Southern Cross". Polychaeta. *Trustees of the British Museum (Natural History) London*, 12, 262–283.