

Biodiversity of echinoids and their epibionts around the Scotia Arc, Antarctica

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Abstract: The Scotia Arc, linking the Magellan region with the Antarctic Peninsula, comprises young and old islands both near continents and isolated, and is the only semi-continuous link between cool temperate and Antarctic environments. It is an ideal region for studies on how marine biodiversity changes across an extended transition zone. Echinoids (sea urchins) and their associated epibionts were found across depths from 91–1045 m, with 19 species from shelf and four from slope depths. The 23 species from 38 trawls represent 31% of all echinoid species known from the Southern Ocean and 38% of the shelf/upper slope echinoids. The specimens collected comprise representatives of the five families Cidaridae, Echinidae, Temnopleuridae, Schizasteridae and Pourtalesiidae. Echinoids are probably a good model for how well we know Antarctic shelf and slope megabenthos; none of the species we report are new to science but we found nine (39%) of our study species present at new localities, some thousands of kilometres from previous findings. New biogeographic ranges are illustrated for *Ctenocidarid gigantea*, *C. nutrix*, *C. spinosa*, *Abatus curvidens*, *A. ingens*, *A. shackletoni*, *Amphineustes rostratus*, *Tripylaster philippi* and *Pourtalesia aurorae*. Southern Ocean echinoids show eurybathy as the mean depth range of our study species was 1241 m and only one was at less than 500 m. The current view of echinoid dominance of super-abundance in the shallows seems to be not transferable to shelf and slope depths as only one of 38 trawls was dominated by echinoids. Current knowledge on maximum sizes in Antarctic echinoids seems to be good as our morphometric measurements were mainly within known size ranges. Regular echinoids increased predictably in mass with increasing test length, apart from *Ctenocidarid spinosa*. Tissue mass of cidaroid species was ~17%, but across irregular species varied from 17.7–8.9%. No epibionts were found on irregular echinoids or Echinidae but 70 cidaroids examined carried 51 species representing ten classes. Many of these species are reported as cidaroid epibionts for the first time. Cidaroids and their epibionts constituted > 38% of the total macrofaunal richness in the trawls they were present in. Echinoids and their epibionts clearly contribute significantly to Southern Ocean biodiversity but are minor components of biomass except in the shallows.

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Key words: biomass, biogeography, echinoids, epibiota

Introduction

Across the world's marine habitats, from young to old, tropics to poles and shores to deep trenches, echinoid echinoderms (sea urchins) are a common and important component of seabed communities. They can be voracious grazers so that high abundance and biomass often results in them playing a major role in structuring benthic communities (Tuya *et al.* 2004 and references therein). They are particularly abundant and ecologically pivotal in kelp forests but also on the nearshore shelf around Antarctica, where they are often the most obvious megafauna. The first specimens were collected during the voyage of HMS *Challenger* in 1873–76 and most of the

Antarctic and sub-Antarctic species were described in the first decades of the twentieth century (David *et al.* 2005a). In the Southern Ocean, the regular urchin *Stereochinus neumayeri* frequently dominates the shallows and a wide variety of species including pencil and burrowing urchins frequent the shelf, slope, abyssal plains and trenches (e.g. Brockington *et al.* 2001, Mooi *et al.* 2004, David *et al.* 2005a, 2005b, Brandt *et al.* 2007a, Palma *et al.* 2007).

The dominance of *S. neumayeri* in the zone accessible to sampling has made it one of the principal model species for studies of Antarctic benthos (e.g. Pearse & Giese 1966, Bosch *et al.* 1987, Brey & Gutt 1991, Brey *et al.* 1995, Tyler *et al.* 2000, Brockington & Peck 2001, Cox & Halanych 2005, Linse *et al.* 2006a, Brockington *et al.* 2007). However, with the exception of a few other species,

This publication is dedicated to the memory of Dr Helen R. Wilcock for whom to visit Antarctica was a lifelong dream.

Table I. Station list of JR 144 BIOPEARL containing echinoids.

| Station | Region | Depth (m) | Date | Latitude S | | Longitude W | |
|------------|------------------------|------------|------------|------------|-----------|-------------|-----------|
| | | | | start | end | start | end |
| FT-AGT-1B | Falkland Islands | 201–197 | 27/02/2006 | 54°18.87' | 54°18.80' | 56°40.75' | 56°41.06' |
| FT-AGT-2 | Falkland Islands | 509–506 | 28/02/2006 | 54°18.07' | 54°17.98' | 56°29.43' | 56°29.82' |
| LI-AGT-2B | Antarctic Peninsula | 870–1013 | 03/03/2006 | 62°20.07' | 62°19.89' | 61°39.21' | 61°39.56' |
| LI-AGT-3 | Antarctic Peninsula | 434–556 | 04/03/2006 | 62°23.77' | 62°23.73' | 61°45.75' | 61°46.28' |
| DI-RGBT-01 | Antarctic Peninsula | 199–209 | 06/03/2006 | 62°55.02' | 62°52.45' | 60°59.56' | 61°00.04' |
| DI-AGT-1 | Antarctic Peninsula | 148–156 | 06/03/2006 | 62°56.85' | 62°05.69' | 60°37.65' | 60°38.00' |
| EI-AGT-3 | Antarctic Peninsula | 463–482 | 12/03/2006 | 61°23.15' | 61°23.24' | 55°01.15' | 55°11.99' |
| EI-AGT-4 | Antarctic Peninsula | 200–199 | 12/03/2006 | 61°20.03' | 61°20.09' | 55°12.04' | 55°12.04' |
| EI-AGT-2 | Antarctic Peninsula | 990–976 | 12/03/2006 | 61°34.52' | 61°03.46' | 55°15.38' | 55°16.08' |
| EI-RGBT-04 | Antarctic Peninsula | 91 | 13/03/2006 | 61°11.57' | 61°09.55' | 55°42.12' | 55°44.48' |
| EI-RGBT-03 | Antarctic Peninsula | 95–88 | 13/03/2006 | 61°11.57' | 61°10.23' | 55°42.36' | 55°44.26' |
| EI-RGBT-06 | Antarctic Peninsula | 14/03/2006 | 61°11.42' | 61°14.22' | 55°44.29' | 55°40.55' | 55°40.55' |
| PB-AGT-4 | South Orkney Islands | 221–211 | 18/03/2006 | 60°49.07' | 60°49.24' | 46°29.38' | 46°29.18' |
| PB-AGT-3 | South Orkney Islands | 506–506 | 18/03/2006 | 60°59.66' | 60°59.41' | 46°49.90' | 46°49.90' |
| PB-AGT-2 | South Orkney Islands | 964–1012 | 18/03/2006 | 61°02.13' | 61°01.76' | 46°51.91' | 46°51.91' |
| SG-RGBT-01 | South Orkney Islands | 240–257 | 23/03/2006 | 60°59.20' | 61°00.03' | 45°54.08' | 45°51.53' |
| SG-RGBT-03 | South Orkney Islands | 154–150 | 24/03/2006 | 60°44.08' | 60°41.57' | 45°29.59' | 45°28.58' |
| SG-RGBT-02 | South Orkney Islands | 235–216 | 24/03/2006 | 60°52.28' | 60°49.47' | 45°30.02' | 45°29.23' |
| ST-AGT-2 | South Sandwich Islands | 1033–1045 | 28/03/2006 | 59°30.45' | 59°30.36' | 27°18.28' | 27°18.98' |
| SG-AGT-4 | South Georgia | 226–224 | 05/04/2006 | 53°36.66' | 53°36.66' | 37°52.64' | 37°52.96' |
| SR-AGT-3 | Shag Rocks | 451–467 | 11/04/2006 | 53°35.10' | 53°35.12' | 40°55.36' | 40°55.25' |
| SR-AGT-4 | Shag Rocks | 212–203 | 11/04/2006 | 53°37.78' | 53°37.70' | 40°54.14' | 40°54.40' |

e.g. *Abatus cordatus* (Schatt & Féral 1991, 1996, Poulin & Féral 1995) or *A. ingens* (Thomson & Riddle 2005), other studies of Antarctic and sub-Antarctic echinoids have simply documented their importance in the composition of macrobenthic assemblages (e.g. Arnaud *et al.* 1998, Ramos 1999, Barnes & Brockington 2003, Rehm *et al.* 2006, Griffiths *et al.* 2008) or their diversity of reproductive modes (e.g. Poulin *et al.* 2002, Chenuil *et al.* 2004, Pearse & Lockhart 2004 and references therein). Even then such studies have already shown this taxon to provide powerful insight into differences between evolutionary and ecological success and glacial versus interglacial selective pressures (Poulin *et al.* 2002).

The extreme physical disturbance around Antarctica (poor fossilization conditions) and rarity of rock uncovered by ice (few areas of exposed fossils) combine to produce a very poor record of faunal change through time in the Southern Ocean. With strong calcified tests and spines, the Echinoidea have one of the better fossil records of the region, from the Cretaceous to the Holocene (e.g. Hotchkiss 1982, Blake & Aronson 1998, Néraudeau *et al.* 2000, BAS Fossil database - Griffiths, personal communication 2007). Their large size, ease of sampling with benthic trawls and ease of identification makes them an ideal group to investigate current and past biodiversity patterns around Antarctica and what underlies them. Some recent studies have assembled species lists for a few markedly different localities, such as the eastern Weddell Sea, Deception Island, the Ross Sea and along the coast adjacent to Victoria Land (see Jacob 2001, Lovell & Trego 2003, Chiantore *et al.* 2006, De Domenico *et al.* 2006). The database of Southern Ocean echinoids

assembled by David *et al.* (2005a), one of the best for any Antarctic taxa, still reveals major gaps in the geographic and bathymetric distributions of many species.

Probably the single most interesting region within the Southern Ocean for marine biogeographic and evolutionary links between the Antarctic and a neighbouring continent is the Scotia Arc. It encompasses islands (and thus shelf areas) of widely different ages and isolation levels and is the only semi-continuous shelf and slope link to a temperate region. It has become an important focus for many research programmes on benthos including the Spanish Antártida 8611 (Ramos 1999), German LAMPOS (Arntz & Brey 2003), international IBMANT (Arntz & Rios 1999, Arntz *et al.* 2005a, 2005b) and British BIOPEARL (Linse 2008) scientific cruises. In the current study we investigate the echinoids living on seven island slopes. We sampled from the continental shelf to the upper continental slope around all the major archipelagos of the Scotia Arc and report the most comprehensive geographic and bathymetric surveys to date for a region of the Southern Ocean. Furthermore, we examine the contribution that echinoids make to Antarctic benthic richness through their considerable associated commensal fauna.

Materials and methods

Study area

Specimens of regular and irregular Echinoidea were collected during the scientific cruise JR 144 (BIOPEARL) of RRS *James Clark Ross* around the Scotia Arc in 2006. Our

sample localities included the Falkland Trough (FT) and six areas south of the Polar Front (Table I). In the South Shetland Islands (SH) we sampled at Deception Island (DI) and Livingston Island (LI) and to the north-east of these at Elephant Island (EI) and Powell Basin (PB). East from there we sampled the southernmost of the South Sandwich Islands (SSI) - Southern Thule Island and finally adjacent to South Georgia (SG) and Shag Rocks (SR) at the northernmost limit of the polar frontal zone. For brevity throughout this study we refer to other localities in the region using the abbreviations: Adelie Land (AD), Antarctic Peninsula (AP), Bellingshausen Sea (BS), Bouvet Island (BI), Cape Horn/Magellan Region (CH/MR), Davis Sea (DS), Dronning Maud Land (DM), Falkland Islands (FI), Kerguelen Islands (KI), Lazarev Sea (LS), eastern Weddell Sea (E-WS), western Weddell Sea (W-WS), Ross Sea (RS), and South Orkney Islands (SO). Within the Scotia Arc are islands with widely varying degrees of isolation and age, and some of the volcanos have even had considerable eruptions within the last few decades (Smellie *et al.* 1998).

Sampling

Benthic samples were taken by two different types of bottom trawls; Agassiz trawl (AGT) and rough bottom otter trawl (RBOT) at 24 stations between depths of 91–1045 m (Table I). When the samples reached the deck, echinoids were separated by hand from other taxa and into families. Of each species collected three specimens were fixed in 96% ethanol, and further specimens of each species were frozen at -20°C . Identities were later established to species level following literature keys.

Morphometric and biomass analysis

Measurements of test length, width and height were made on each individual or each species using digital Vernier callipers to accuracy levels of 1 mm. In total 273 regular (cidaroid and temnopleurid) and irregular (spatangoid and holasteroid) specimens from 24 locations were measured (Table II). Population size spectra and shape variability (ratios of length, width and height measurements) were compared within and between species and locations. In cidaroid specimens all spines were removed before mass measurements for comparability between specimens as some had either incomplete numbers of spines or epibionts on the spines. Dry mass and ash free dry mass measurements were obtained exclusively from frozen samples. Only the tests of species represented by at least 10 individuals were ashed to obtain ash free dry mass measurements as intact representatives of each species were considered as rare and valuable reference material.

Our definitions were as follows,

Wet mass (WM): individuals were unfrozen and pressed onto tissue paper to remove excess moisture for 30

seconds. Their wet mass was then determined to accuracies of 0.001 g.

Dry mass (DM): individuals were oven dried at 60°C for 24 hours in pre-weighed tin foil receptacles. Specimens were allowed to cool to ambient temperature. Thereafter specimens were again measured to accuracies of 0.001 g.

Ash-free dry mass (AFDM): dried individuals were placed in a furnace at 480°C for 24 hours in pre-weighed tin receptacles. Specimens were allowed to cool to ambient temperature in a desiccator containing silica gel. Thereafter specimens were transferred to a microbalance (Satorius MC210P) and the ash measured to accuracies of 0.001 g. The ash mass was then subtracted from the previously recorded DM for each specimen to yield the AFDM to accuracies of 0.001 g.

Despite masses being recorded to 0.001 g accuracy, we only report these to 0.1 g levels due to inherent inaccuracies, such as variation in gut contents across individuals.

Epibiont analysis

Specimens of every species from every site were examined for epifaunal colonists. Up to 24 individuals of each species were studied for attached macrofauna using a binocular microscope. In most cases at least some spines had been lost during the process of being trawled, brought to the surface and landed on the ship's deck. Where a species was represented by many individuals at a site, the most intact specimens were examined. On the echinoids with epifauna (cidaroid species), the colonists were identified to the lowest possible taxonomic level, in most cases species. Each epifaunal species was scored as abundant (present on all specimens examined), occasional (present on $<$ all but $>$ 1 individual) or rare (present on just 1 individual).

Results

Echinoidea were present, sometimes abundant but rarely a dominant component of most shelf trawls at locations around the Scotia Arc. Echinoids were rarely present in any of the continental slope trawls (\sim 1000 or 1500 m depths) but at the Southern Thule site (deep sea) echinoids were only found at 1000 m. Otherwise echinoids were absent from some study depths at some locations but only at South Georgia did they dominate the benthos (Table II). In total 13 species of regular urchins (Fig. 1a) and 10 species of irregular urchins (Fig. 1b) were found. These collections greatly extended the distribution and depth ranges, by thousands of km and hundreds of metres respectively, for several species.

Distribution and biometrics of Scotia Arc echinoid species

Where our data extend the depth, test size and/or geographic distribution ranges of echinoid species or the epibiont taxa

Table II. Echinoid species per station.

| Station | FT-AGT-1B | FT-AGT-2 | LI-AGT-2B | LI-AGT-3 | DI-RGBT-01 | DI-AGT-1 | EI-AGT-3 | EI-AGT-4 | EI-AGT-2 | EI-RGBT-04 | EI-RGBT-03 | EI-RGBT-06 |
|------------------------------------|-----------|----------|-----------|----------|------------|----------|----------|----------|----------|------------|------------|------------|
| Cidaridae | | | | | | | | | | | | |
| <i>Aporocidaris cf eltaniana</i> | | | | | | | | | x | | | |
| <i>Austrocidaris aff spinulosa</i> | x | x | | | | | | | | | | |
| <i>Notocidaris mortenseni</i> | | | | | | | | x | | | | |
| <i>Ctenocidaris gigantea</i> | | | | | x | | | x | | | | |
| <i>Ctenocidaris perrieri</i> | | | | | x | | | | | | | |
| <i>Ctenocidaris rugosa</i> | | | | | | | | x | | | | x |
| <i>Ctenocidaris nutrix</i> | | | | | | | | | | | | |
| <i>Ctenocidaris spinosa</i> | | | | | x | | | | | | | |
| <i>Ctenocidaris speciosa</i> | | | | | | | | | | | | |
| Cidaridae indet | | | | | x | | | | x | x | | |
| Echinidae | | | | | | | | | | | | |
| <i>Sterechinus agassizi</i> | x | x | | | | | | | | | | |
| <i>Sterechinus antarcticus</i> | | | | | | | | | | | | |
| <i>Sterechinus neumayeri</i> | | | | | | x | | | | | | |
| Temnopleuridae | | | | | | | | | | | | |
| <i>Pseudechinus magellanicus</i> | x | | | | | | | | | | | |
| Schizasteridae | | | | | | | | | | | | |
| <i>Abatus cavernosus</i> | | | | | | | | | | | | |
| <i>Abatus curvidens</i> | | | | | | | | | | | | |
| <i>Abatus elongatus</i> | | | | | | | | | | | | |
| <i>Abatus ingens</i> | | | | | x | | x | x | | x | | |
| <i>Abatus sp</i> | | | | | | | | x | | | | |
| <i>Amphineustes cf lorioli</i> | | | | | | | | | | | | |
| <i>Amphineustes rostratus</i> | | | | | x | | | | | | | |
| <i>Brachysternaster chesheri</i> | | | | | x | | | | | | | |
| <i>Genicopatagus affinis</i> | | | | | | | | x | | | | |
| <i>Tripylaster philippii</i> | | | | | | | | | | | x | |
| Schizasteridae indet | | | x | x | | | | | x | | | |
| Pourtalesiidae | | | | | | | | | | | | |
| <i>Pourtalesia aurorae</i> | | | | | | | | | | | | |

known from them we show this information in **bold**. General information for echinoid species on distribution, depth, size and ecology was taken from David *et al.* (2005a) and our new findings were added.

Order Cidaroida
 Family Cidaridae
Aporocidaris cf eltaniana Mooi, David, Fell & Chone, 2000

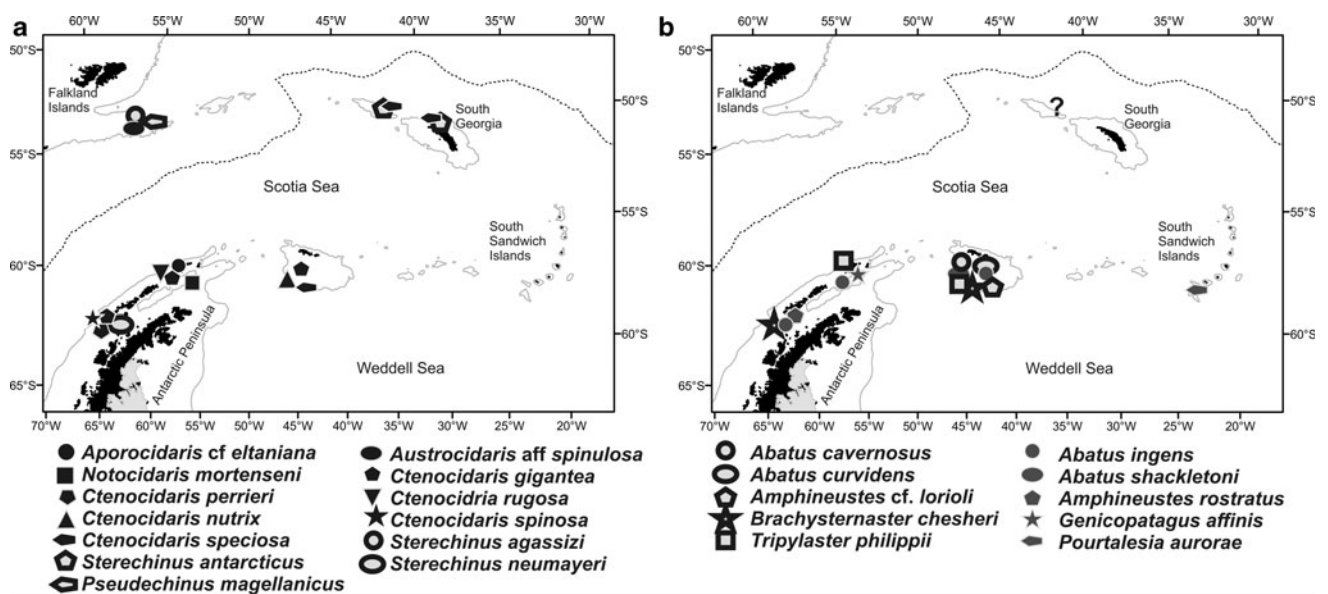


Fig. 1. Distributions of echinoids collected during the BIOPEARL cruise **a.** regular echinoids, **b.** irregular echinoids.

Table II. (Continued) Echinoid species per station.

| Station | PB-AGT-4 | PB-AGT-3 | PB-AGT-2 | SG-RGBT-01 | SG-RGBT-03 | SG-RGBT-04 | SG-RGBT-02 | ST-AGT-2 | SG-AGT-3 | SG-AGT-4 | SR-AGT-3 | SR-AGT-4 |
|------------------------------------|----------|----------|----------|------------|------------|------------|------------|----------|----------|----------|----------|----------|
| Cidaridae | | | | | | | | | | | | |
| <i>Aporocidaris cf eltaniana</i> | | | | | | | | | | | | |
| <i>Austrocidaris aff spinulosa</i> | | | | | | | | | | | | |
| <i>Notocidaris mortenseni</i> | | | | | | | | | | | | |
| <i>Ctenocidaris gigantea</i> | | x | | | | | | | | | | |
| <i>Ctenocidaris perrieri</i> | | | | | | | | | | | | |
| <i>Ctenocidaris rugosa</i> | | | | | | | | | | | | |
| <i>Ctenocidaris nutrix</i> | | x | | | | | | | | | | |
| <i>Ctenocidaris spinosa</i> | | | | | | | | | | | | |
| <i>Ctenocidaris speciosa</i> | | x | x | | | | | | x | | x | x |
| Cidaridae indet | | | | x | x | | | | | | | |
| Echinidae | | | | | | | | | | | | |
| <i>Sterechinus agassizi</i> | | | | | | | | | | | | |
| <i>Sterechinus antarcticus</i> | | | | | | | | | x | x | x | x |
| <i>Sterechinus neumayeri</i> | | | | | | | | | | | | |
| Temnopleuridae | | | | | | | | | | | | |
| <i>Pseudechinus magellanicus</i> | | | | | | | | | | | | |
| Schizasteridae | | | | | | | | | | | | |
| <i>Abatus cavernosus</i> | | | | | | | | | | x | | |
| <i>Abatus curvidens</i> | | | | | | x | x | | | x | | |
| <i>Abatus elongatus</i> | | | | | | | | | | | | |
| <i>Abatus ingens</i> | x | | | | | | x | | | | | |
| <i>Abatus sp</i> | x | | | | | | x | | | x | | |
| <i>Amphipneustes cf lorioli</i> | | | x | | | | | | | | | |
| <i>Amphipneustes rostratus</i> | | | | | | | | | | | | |
| <i>Brachysternaster chesheri</i> | | | | | x | | | | | | | |
| <i>Genicopatacus affinis</i> | | | | | | | | | | | | |
| <i>Tripylaster philippii</i> | x | | | | | | | | | | | |
| Schizasteridae indet | x | | | | | | | | | | | x |
| Pourtalesiidae | | | | | | | | | | | | |
| <i>Pourtalesia aurorae</i> | | | | | | | | | x | | | |

Distribution SH (LI 1437 m, EI 884–990 m)
 Depth 884–1437 m
 Size up to 45 mm horizontal diameter, holotype: 29.3 mm in diameter, 16.9 mm height
 Remarks Two specimens of *Aporocidaris cf eltaniana* were collected at 884–990 m at Elephant Island, the shallowest the species has been reported to date.

Austrocidaris aff spinulosa Mortensen, 1910

Distribution off CH/MR (30–641 m), FI (124–509 m), SG (13–45 m)
 Depth 13–641 m
 Size up to **35 mm horizontal Ø** (previous 31 mm Ø)
 Remarks The specimens, collected on the shelf in the Falkland Trough, resemble *Austrocidaris spinulosa* in their overall morphology, though their primary spines have more barbs than is typical. Our specimens showed very little variation in shape but some in mass to length and wet mass was approximately 2.5x dry mass (Figs 2a & 3).

Epibiota They were densely colonized by a diverse range of epibionts, many of which have never been reported either as commensal on echinoids or even other fauna. Their primary spines were colonized by **Annelida (6 polychaete species), Bryozoa (15 cheilostome and 2 cyclostome species), Cnidaria (1 hydroid species), Crustacea (1 isopod species), Mollusca (1 bivalve species), Porifera (2 demosponge species), Foraminifera and foliculinid Protozoa.**

Notocidaris mortenseni (Køehler, 1900)

Distribution SH (EI 192–745 m), SO (284–302 m), E-WS (569–624 m, 587–746 m, 350–602 m), RS (589–714 m, 1225–1240 m), BS (350 m, 100–600 m)
 Depth 100–1240 m
 Size **44 mm horizontal Ø** (previous 40 mm Ø)
 Remarks Wet mass was about 3x dry mass.
 Epibiota Jacob (2001) reported a diverse epifauna from the spines of this species, consisting of spirorbid polychaetes, bryozoans, the bivalve

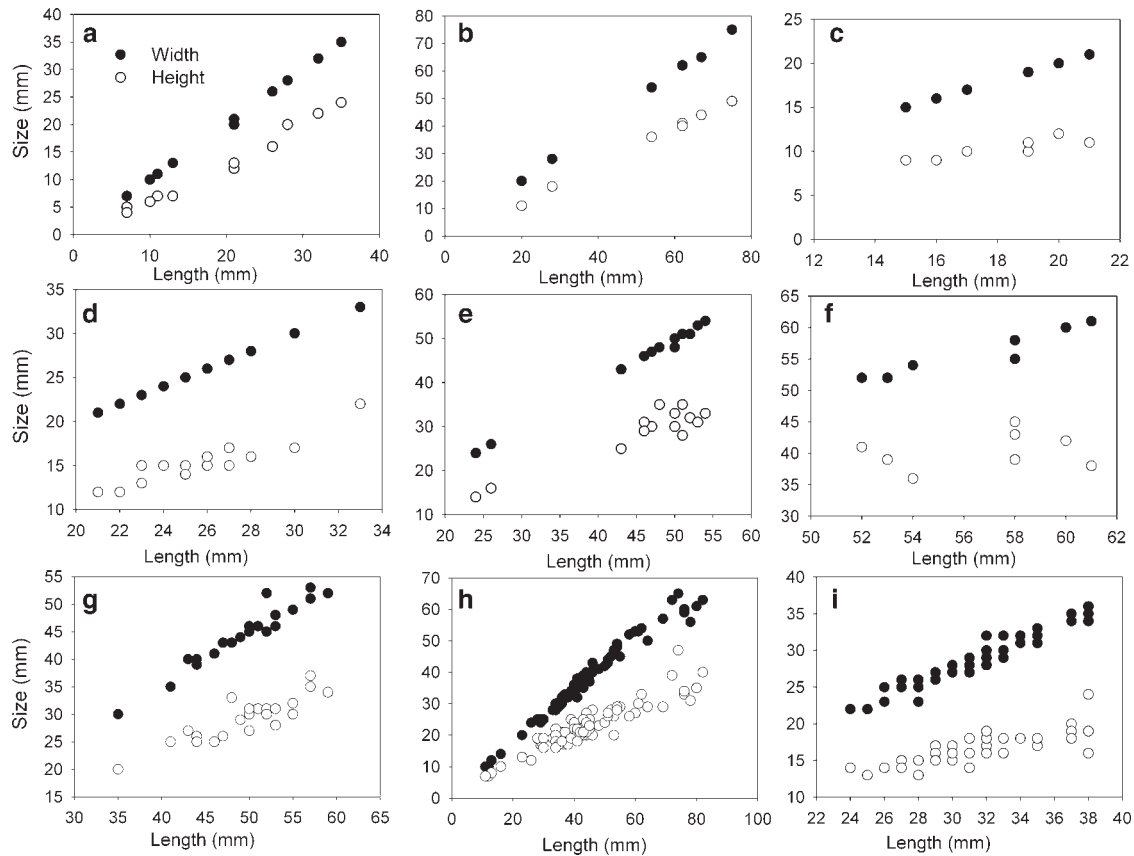


Fig. 2. Test height and width relationships with test length in the regular echinoids **a.** *Austrocidaris* aff. *spinulosa*, **b.** *Ctenocidaris gigantea*, **c.** *C. nutrix*, **d.** *C. rugosa*, **e.** *C. speciosa*, and **f.** *C. spinosa*, and the irregular echinoids **g.** *Abatus curvidens*, **h.** *A. ingens* and **i.** *Tripylaster philippi*.

Lissarca notorcadensis, Holothuroidea, and the sponge *Jophon radiatus*. This study found representatives of all known epibiont groups and recorded **serpulid annelids** and **Foraminifera** for the first time.

Ctenocidaris gigantea H.L.Clark, 1925

Distribution SH (LI 199–209 m, EI 199–200 m), SO (232–506 m), E-WS (399–462 m, 294–746 m, 302–531 m), DS (540 m), RS (190–375 m, 184–320 m, 256–384 m, 238–340 m, 408–565 m, 344–357 m)

Depth 184–746 m

Size up to 65 mm in diameter

Remarks This is the first record of *C. gigantea* for the South Shetland Islands. Our specimens showed little variation in shape or mass to length. Typically wet mass was about 5x dry mass but two large individuals of similar dry mass did have quite different wet masses (Figs 2b & 3).

Epibiota The known epifauna consists of the bivalve *L. notorcadensis*, the sponge *J. radiatus* and bryozoans (Jacob 2001) while this study also

found **Annelida (1 spirorbid and 1 serpulid species)**, **Chordata (1 ascidian species)** and **Foraminifera**.

Ctenocidaris perrieri K  hler, 1912

Distribution AP (450–670 m), SH (LI 32–750 m, EI 73–1230 m), SO (232–662 m), SSI (148–201 m), W-WS (31–704 m), E-WS (498–509 m, 193–898 m, 185–423 m), DM (207–216 m, 300 m), DS (220 m, 219 m), AL (293–329 m), RS (64–836 m)

Depth 31–1230 m

Size 50 mm diameter, up to 70 mm diameter

Remarks The following epibiotic groups are previously known to occur on this species: foraminiferans, sponges, polychaetes, bivalves, brachiopods, bryozoans, small crinoids and holothurians.

Ctenocidaris nutrix (Thomson, 1876)

Distribution SO (506 m), E-WS (270–509 m, 294–305 m, 301–403 m), DM (200–450 m), DS (450–530 m), KI (250–450 m)

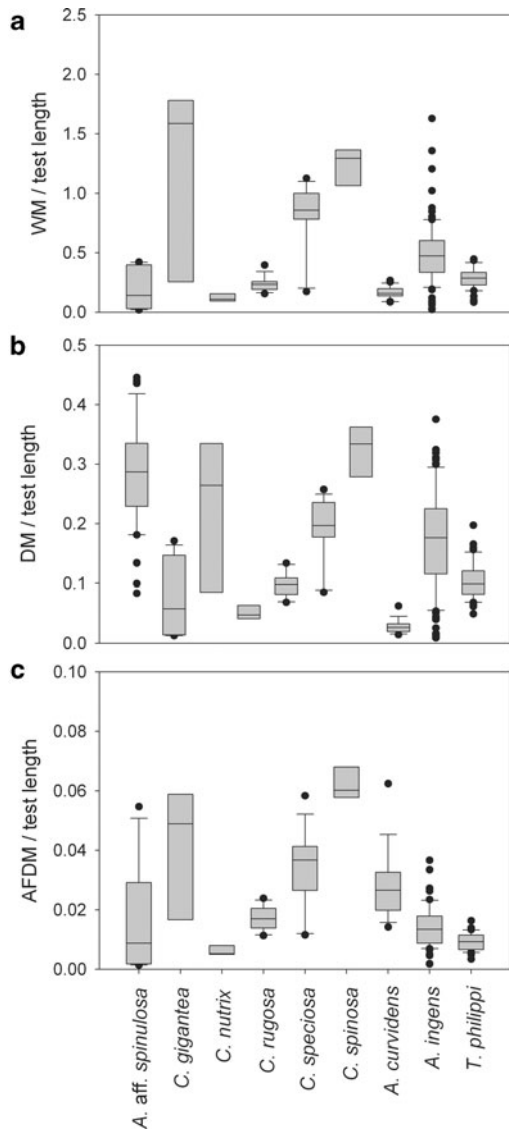


Fig. 3. Mass relationships with test length in regular and irregular echinoids for **a.** wet mass (WM), **b.** dry mass (DM), and **c.** ash free dry mass (AFDM).

Depth 23–650 m
 Size 30–40 mm diameter
 Remarks This is the first record for the species from the South Orkney Islands. Height at size varied more than length to width and typically wet mass was 2.6x dry mass but one specimen had anomalously low mass for its size (Figs 2c & 3).
 Epibiota Despite being small, *C. nutrix* was host to a diverse array of epibionts on the primary spines including **Annelida, Bryozoa, Cnidaria** and **Foraminifera**.

Ctenocidaris rugosa (Køehler, 1926)

Distribution SH (EI 199–267 m), SO (232–239 m), E-WS (233–406 m, 437–810 m), DS (442–598 m) AL (278–651 m)
 Depth 199–810 m
 Size 71 mm diameter
 Remarks As in *C. nutrix*, height varied more than width in its relation to length. Mass to length ratio varied little and wet mass to dry mass ratios (Figs 2d & 3) were similar to *C. nutrix* and *Austrocidaris cf spinulosa*.
 Epibiota No epibionts were known from this species but we found a **polychaete, crustacean, echinoderm, bivalve** and **foraminifera**.

Ctenocidaris speciosa Mortensen, 1910

Distribution FI (339–357 m), SH (LI 160–500 m, EI 192–1120 m), SO (232–761–**1012 m**), SSI (148–201 m), SG (75–686 m), SR (160–**467 m**), W-WS (203–512 m, 400 m), E-WS (498–624 m, 587–1353 m, 602–617 m)
 Depth 75–1353 m
 Size typically 50 mm diameter, but up to 62 mm diameter
 Remarks We established new depth records for three sites in this widely occurring species. Length

Table III. Individual size measurements of the rare irregular echinoid species.

| Species | Specimen no. | Length (mm) | Width (mm) | Height (mm) |
|-----------------------|---------------|-------------|------------|-------------|
| <i>A. cavernosus</i> | BAS 06-664-09 | 49 | 48 | 32 |
| | BAS 06-664-10 | 48 | 47 | 30 |
| <i>A. shackletoni</i> | BAS 06-678-06 | 53 | 47 | 33 |
| | BAS 06-678-15 | 58 | 50 | 36 |
| <i>A. cf lorioli</i> | BAS 06-602-01 | 46 | 38 | 26 |
| | BAS 06-602-02 | 48 | 44 | 26 |
| <i>A. rostratus</i> | BAS 06-269 | 71 | 54 | 43 |
| <i>B. chesheri</i> | BAS 06-678-08 | 58 | 53 | 36 |
| | BAS 06-678-14 | 45 | 38 | 29 |
| | BAS 06-678-19 | 57 | 51 | 35 |
| | BAS 06-273-02 | 74 | 64 | 46 |
| | BAS 06-273-05 | 70 | 63 | 41 |
| | BAS 06-273-09 | 61 | 54 | 37 |
| | BAS 06-273-10 | 85 | 65 | 39 |
| | BAS 06-273-11 | 75 | 60 | 43 |
| | BAS 06-273-14 | 65 | 55 | 40 |
| | BAS 06-273-15 | 59 | 50 | 37 |
| <i>G. affinis</i> | BAS 06-472-03 | 25 | 23 | 15 |
| | BAS 06-472-04 | 20 | 17 | 12 |
| | BAS 06-472-12 | 25 | 23 | 13 |
| | BAS 06-472-44 | 26 | 25 | 14 |
| | BAS 06-472-59 | 28 | 26 | 17 |
| <i>P. aurorae</i> | BAS 06-744-01 | 42.7 | 23.2 | 21.2 |
| | BAS 06-744-02 | 44.9 | 28.0 | 24.5 |
| | BAS 06-744-03 | 50.6 | 33.0 | 30.0 |

Table IV. Echinoid epibionts. Abbreviations: (x) - number of analysed echinoid specimens, ● - abundant, ⊗ - occasional, ○ - rare.

| Epibiota | <i>A.</i> , cf. <i>spinulosa</i> | <i>C. gigantea</i> | | <i>C. nutrix</i> | <i>C. rugosa</i> | <i>C. speciosa</i> | | <i>C. spinosa</i> | | <i>N. m</i> |
|---------------------------------|----------------------------------|--------------------|--------|------------------|------------------|--------------------|--------|-------------------|--------|-------------|
| | FT (14) | DI (4) | PB (3) | PB (7) | EI (17) | PB (5) | SR (9) | PB (2) | DI (8) | EI (1) |
| <i>Annelida</i> | | | | | | | | | | |
| <i>Polychaeta</i> | | | | | | | | | | |
| <i>Paralaeopsira cavata</i> | ⊗ | | | | | | | | | |
| <i>P. levinseni</i> | ● | ⊗ | ⊗ | | | | | | | ○ |
| <i>P. moerchi</i> | ⊗ | | ⊗ | | | | | | | |
| <i>P. patagonica</i> | ○ | | | | | | | | | |
| <i>Romanchella perrieri</i> | | | | | | | | | | ○ |
| <i>Serpula narconensis</i> | ○ | | | | | | | | | |
| Serpulidae | ⊗ | ● | | | | | | | | ○ |
| Unknown | | | | | ○ | | | ⊗ | | |
| <i>Bryozoa</i> | | | | | | | | | | |
| <i>Cheilostome</i> | | | | | | | | | | |
| <i>Arachnopusia aviculifera</i> | | ○ | | | | | | | | |
| <i>Cellaria diversa</i> | ○ | | ○ | | | | | ⊗ | | |
| <i>C. malvinensis</i> | ○ | | | | | | | | ○ | |
| <i>Celleporella Antarctica</i> | | | | | | | ○ | | | |
| <i>C. bougainvillea</i> | | | ○ | | | | | | | ○ |
| <i>Cornucopina pectogamma</i> | ● | | | | | | ○ | | | |
| <i>Escharoides torquata</i> | | | | | | | | | | ○ |
| <i>Fenestulina crystallina</i> | | | | | | | | | | ○ |
| <i>Himantozoum obtusum</i> | ○ | | ○ | | | | | | | |
| <i>Menipea flagellifera</i> | ⊗ | | | | | | | | | |
| <i>Micropora brevissima</i> | ○ | | | | | | | | | ○ |
| <i>Microporella hyadesi</i> | ⊗ | | | | | | | | | |
| <i>Orthoporida compacta</i> | ○ | | | | | | | | | |
| <i>Osthimosia sp.</i> | ⊗ | ⊗ | | | | | ⊗ | | | |
| <i>O. bicornis</i> | ⊗ | | ○ | | | | ⊗ | | | ○ |
| <i>O. curtioscula</i> | ○ | | ○ | | | | | ● | | |
| <i>O. malingae</i> | ⊗ | | | | | | | | ○ | |
| <i>O. phalacrocoraca</i> | ○ | | | | | | ○ | | | |
| <i>Parasmittina elephantine</i> | | | | | | | | | ○ | |
| <i>Smittina anecdota</i> | | | | | | | | | | ○ |
| <i>S. Antarctica</i> | ○ | | | | | | | | | |
| <i>S. glebula</i> | | ○ | | | | | | | ○ | |
| <i>S. incernicula</i> | | | | | | | ○ | | | |
| <i>S. obicullata</i> | | | | | | | | | ○ | |
| <i>Smittoidea conspicua</i> | | | | | | | | | ○ | |

to width varied very little but height to length varied considerably (Figs 2e & 3). Wet mass was $\geq 4x$ dry mass.

Epibiota Prior to this study only *L. notorcadensis* was known as a spine epibiont of this echinoid species but the current study found at least 13 species on 14 specimens. Epibionts included **Bryozoa, Crustacea, Echinodermata, Porifera** and **Foraminifera**.

Ctenocidaris spinosa (Køehler, 1926)

Distribution **SH (LI 199–209 m)**, E-WS (64–423 m, 893–898 m, 210–233 m, 390–396 m), LS (200–300 m), DS (202 m)

Depth 64–898 m

Size typically 40–50 mm diameter, up to 52 mm diameter

Remarks This is the first record of *C. spinosa* from the South Shetland Islands and even western Antarctica. Of the cidaroid echinoids, this species varied most in height to length, such that no relationship was evident while the mass/test length relationships were less variable (Figs 2f & 3).

Epibiota Jacob (2001) reported Bryozoa, the bivalve *L. notorcadensis*, holothuroidea, and the sponge *J. radiatus* to occur as epibionts of *C. spinosa*. In addition Hétériet *et al.* (2004) found Annelida, Cnidaria and Foraminifera. In total the current study found 10 specimens

Table IV. (Continued) Echinoid epibionts. Abbreviations: (x) - number of analysed echinoid specimens, ● - abundant, ⊗ - occasional, ○ - rare.

| Epibiota | <i>A.</i> , cf. <i>spinulosa</i> | <i>C. gigantea</i> | | <i>C. nutrix</i> | <i>C. rugosa</i> | <i>C. speciosa</i> | | <i>C. spinosa</i> | | <i>N. m</i> |
|-------------------------------|----------------------------------|--------------------|--------|------------------|------------------|--------------------|--------|-------------------|--------|-------------|
| | FT (14) | DI (4) | PB (3) | PB (7) | EI (17) | PB (5) | SR (9) | PB (2) | DI (8) | EI (1) |
| <i>Talivittaticella</i> sp. | ○ | | | | | | | | | |
| Ctenostome | | | | | | | | | | |
| <i>Alcyonidium</i> sp | | ⊗ | | | | | ⊗ | | | |
| Cyclostome | ○ | | | | | | | ○ | | |
| <i>Idmidronea</i> sp | ○ | | | | | | | | | |
| Unknown | | | ○ | | | | | | | |
| Chordata | | | | | | | | | | |
| Ascidiacea | | | | | | | | | | |
| <i>Pyura</i> sp | | ○ | | | | | | | | |
| Cnidaria | | | | | | | | | | |
| Hydroidea | | | | | | | | | | |
| <i>Schizotricha</i> sp | | | | | | | | | | |
| Unknown | ○ | | | ⊗ | | | | | ○ | |
| Unknown 2 | | | | ○ | | | | | | |
| Crustacea | | | | | | | | | | |
| Malacostraca | | | | | | | | | | |
| <i>Antarcturus</i> sp | ○ | | | | | ○ | | ○ | | |
| Munnidae | | | | | | | | ○ | | |
| Echinodermata | | | | | | | | | | |
| Holothuroidea | | | | | | | | | | |
| <i>Echinopsolus</i> sp | | | | | | ● | | | ○ | |
| Ophiuroidea | | | | | | | | | ○ | |
| <i>Ophiacantha</i> sp | | | | | | | | ○ | | |
| Mollusca | | | | | | | | | | |
| Bivalvia | | | | | | | | | | |
| <i>Lissarca notorcadensis</i> | | ⊗ | | | | ⊗ | | ⊗ | ● | |
| <i>Philobrya</i> sp | ○ | | | | | | | | | |
| Porifera | | | | | | | | | | |
| Demospongiae | | | | | | | | | | |
| <i>Iophon radiatus</i> | | | | | | | | ⊗ | | |
| Unknown 1 | ○ | | | | | | | | | ○ |
| Unknown 2 | ○ | | | | | | | ⊗ | | |
| Unknown 3 | | | | | | | | | ○ | |
| Foraminifera | ● | ● | | ● | | ⊗ | | ⊗ | ● | ○ |
| Foliculinid | ● | | | | | | | ○ | | |
| Total taxa | 30 | 9 | 0 | 11 | 5 | 0 | 13 | 4 | 15 | 11 |

supported at least 18 epibiont species, of which **foliculinid Protozoa** are new reports.

Order Echinoida
Family Echinidae

Remarks Three species of the genus *Sterechinus* were found around the Scotia Arc. Examination of live specimens of the *Sterechinus* species found (listed below) revealed no epibiota on any specimen of any species. The specimens collected during this expedition are used for a comparative study on the calcium carbonate uptake in shell and test building taxa from temperate and polar regions and are not considered further in this study. Their distribution details are listed below.

Sterechinus agassizi Mortensen, 1910

Distribution FI (103–430–509 m), SR (177–199 m), SG (13–970 m), BI (320–471 m) MI (300–500 m)

Depth 13–970 m
Size up to 80 mm diameter

Sterechinus antarcticus Kœhler, 1901

Distribution circum-Antarctic
Depth 32–2012 m
Size typically 50 mm diameter, but up to 80 mm diameter

Sterechinus neumayeri (Meissner, 1900)

Distribution circum-Antarctic
Depth 0–810 m
Size typically 30 mm diameter, but up to 70 mm diameter

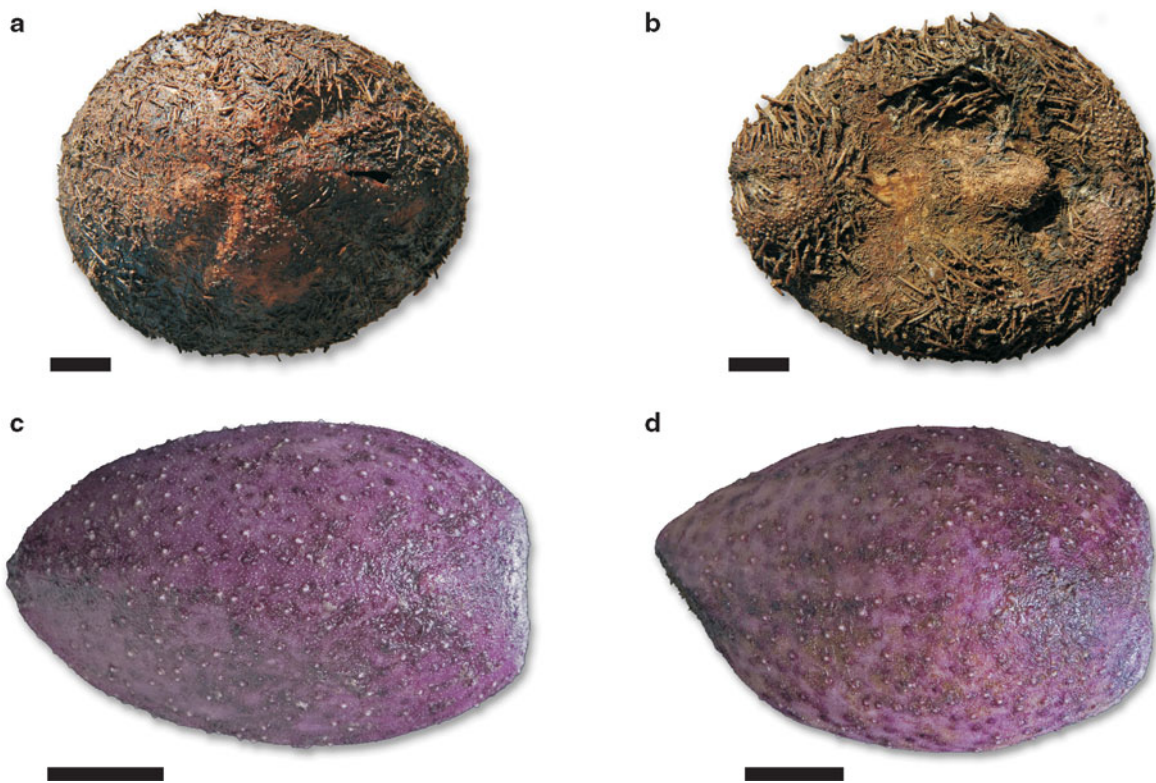


Fig. 4. Specimens of **a. & b.** *Abatus ingens* Kœhler, 1926 and **c. & d.** *Pourtalesia aurorae* Kœhler, 1926. a, b. BAS 06-273-13, c. BAS 06-744-02, d. BAS 06-744-03. Scale bar 10 mm.

Order Temnopleurida

Family Temnopleuridae

Pseudechinus magellanicus (Philippi, 1857)

Distribution off CH/MR (1–10 m, 1–250 m), FI (1–242 m)
 Depth 1–250 m
 Size 25–40 mm diameter
 Epibiota None found.

Order Spatangoida

Family Schizasteridae

Abatus cavernosus (Philippi, 1845)

Distribution SH (LI 160–500 m, EI 19–28 m), SO (11–761 m), SR (3742–3806 m), SG (11–970 m), BI (20–60 m), DS (219 m), AL (20–46 m), off CH/MR (174 m)
 Depth 11–3806 m
 Size max length up to 50 mm.
 Remarks The two specimens found were almost at the maximum size recorded (Table III).
 Epibiota Mortensen (1951) noted commensal bivalves, especially in the marsupial and on the peristome spines but no bivalves or other associated epibiont species were found on

the two specimens collected in this study.

Abatus curvidens Mortensen, 1936

Distribution W-WS (246–500 m), SH (LI 160–670 m, EI 20–769 m), **SO (150–235 m)**
 Depth 20–769 m
 Size max length in males up to 43 mm, max length in females up to 51 mm.
 Remarks This study extends the biogeographic distribution of this species to the South Orkney Islands. There is minor variability in shape, both in length to width and to height (Fig. 2 g). We found wet mass to be an unreliable predictor of dry mass (or AFDM, see Fig. 3).
 Epibiota None known.

Abatus ingens Kœhler, 1926

Distribution **SH (LI 199–209 m, EI 199–482 m), SO (150–235 m)**, DS (333–761 m, 202 m), AL (46 m, 20–30 m), RS
 Depth 20–761 m
 Size length typically 60–70 mm can reach up to 88 mm

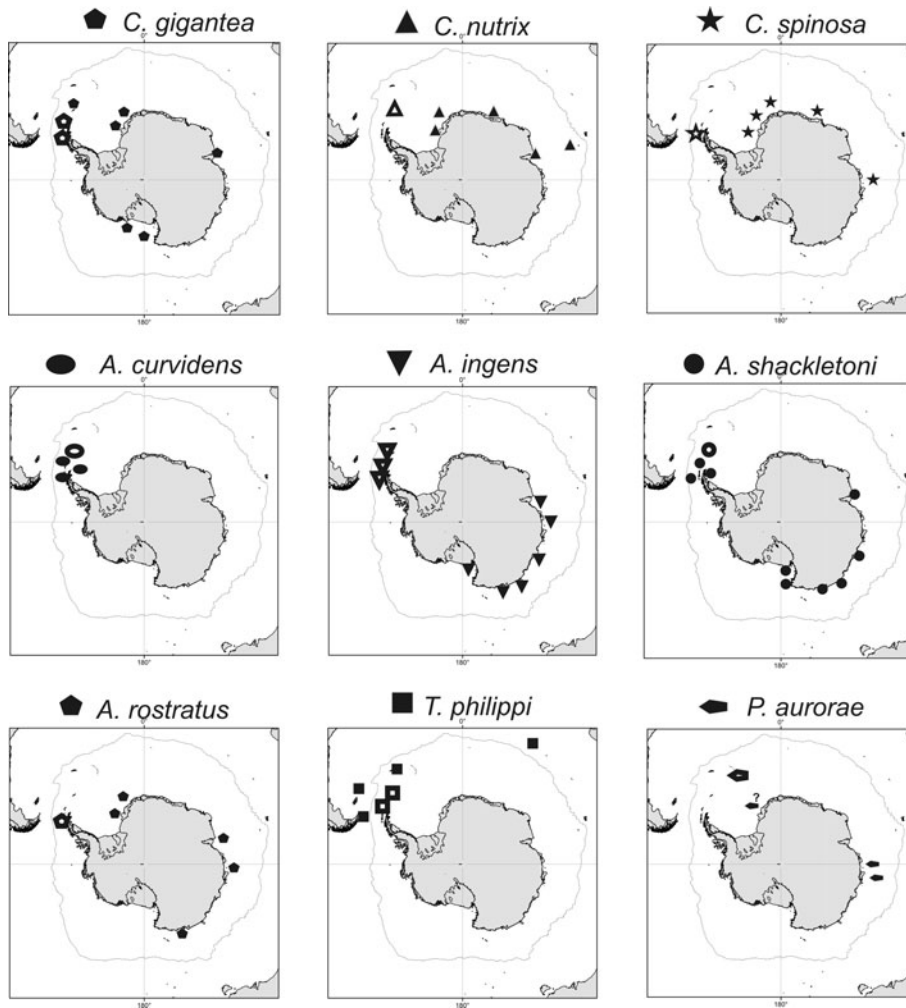


Fig. 5. Biogeographical distributions of echinoid species with new records. Known distribution records are marked in black filled-in labels, new records in open labels.

Remarks This study extends the biogeographical distribution of this species to the South Shetland and South Orkney islands, therefore a representative specimen is figured (Fig. 4a & b). More variability in length to height than vs width (Fig. 2 h). Wet mass measurements showed two distinct patterns possibly male and female, but this was less obvious in dry mass (Fig. 3). The samples of *A. ingens* we found were very large south of Livingston Island (> 60 mm length) whereas those around Powell Basin and South Georgia were small (< 46 mm). North of Livingston Island nearly the entire range of *A. ingens* were found (25–72 mm). Lockart *et al.* (1994) report brooding with up to 149 juveniles in Prydz Bay. In the current collection only two specimens carried young in their marsupia.

Epibiota None known.

Abatus shackletoni K  hler, 1911

Distribution SH (LI 30–92 m, EI), **SO (240–257 m)**, W-WS (51–70 m), DS (8 m, 431 m), AL (35–73 m, 20–46 m, 0–30 m), RS (44–184 m, 13–631 m)

Depth 8–631 m

Size length typically 45 mm but females can reach 67 mm

Remarks First species record for the South Orkney Islands (two specimens). Size measurements for the specimens of *A. shackletoni* collected are given in Table III.

Epibiota None known.

Amphipneustes cf lorioli K  hler, 1901

Distribution BS (300–600 m), SH (LI 70–592 m, EI 174–1230 m), SO (232–**1012 m**), W-WS (137–512 m, 400 m), E-WS (270–462 m, 193–2012 m, 391–623 m), DS (219 m), DS South (474–500 m), RS

Depth 70–2012 m

Size about 50 mm length

Remarks Two specimens resembling *Amphipneustes* cf *lorioli* were collected in the southern slope of the South Orkney Islands, the deepest recorded for this location. Size measurements for the specimens of *A. cf lorioli* collected are given in Table III.

Epibiota No epibiota known.

Amphipneustes rostratus (Køehler, 1926)

Distribution **SH (LI 199–209 m)**, E-WS (399–462 m, 352–1353 m, 406–531 m), DS (532–536 m, 442–598 m, 202–659 m), AL (278–651 m)

Depth **199–1353 m**

Size up to **71 mm** length (previous known 50–60 mm length)

Remarks This is the first record for the South Shetland Islands. The single specimen is the largest example of *A. rostratus* known (Table III).

Epibiota No epibiota known.

Brachysternaster chesheri Larrain, 1985

Distribution SH (LI **199–202–670**, EI 192–745 m), SO (**150–232–239 m**), W-WS (246–320 m), E-WS (270–462 m, 442–1353 m), LS (207–216 m)

Depth **150–1353 m**

Size up to **85 mm** length (typically 55–60 mm lengths, females up to 77 mm)

Remarks At both the South Shetland and South Orkney islands we found *B. chesheri* shallower than has been recorded in the past. Their sizes are shown in Table III and include one specimen which is the largest ever reported.

Epibiota No epibiota known.

Genicopatagus affinis A. Agassiz, 1879

Distribution SH (EI **199–621 m**), SSI (4680–5651), E-WS (1353 m), 60°S 100°E (3607 m)

Depth **199–5651 m**

Size 37 mm length, up to 61 mm

Remarks All five specimens of *G. affinis* collected were smaller than the reported sizes and with 20–28 mm test length similar in size (Table III).

Epibiota No epibiota known.

Tripylaster philippii (Gray, 1851)

Distribution off CH/MR (115 m), FI (74–595 m), **SH (EI 91 m)**, **SO (211–221 m)**, SG (13–45 m), MI (45–570 m)

Depth 13–595 m

Size 78 mm length

Remarks The current study extends the known range of the species to both the South Orkney and South Shetland islands. Shape is fairly variable (Fig. 2i) as is length to dry mass (Fig. 3). Wet mass was a poor predictor of dry mass and was highly variable.

Epibiota No epibiota known.

Order Holasteroidea

Family Pourtalesiidae

Pourtalesia aurorae Køehler, 1926

Distribution **SSI (1033–1045 m)**, DS (442–598 m, 1600 m)

Depth 442–1600 m

Size 44–55 mm

Remarks This species is one of the least known Antarctic echinoderms. Confirmed distributions of this species are only known from two sites in the Davis Sea (David *et al.* 2005a). A record from the Weddell Sea appeared doubtful to David *et al.* (2005a). They stated “It is possible that one specimen, collected in the WS by the RV *Polarstern* and identified as *P. aff hispida* by De Ridder *et al.* (1992), may be *P. aurorae*.” Because their specimen was different from typical *P. aurorae* they did not wish to suggest the dramatic change in its geographic distribution. The three specimens collected during the current cruise were clearly identified as *P. aurorae* by their test morphology and distinct colour (Fig. 4c & d) and extend the species biogeographic range thousands of kilometres beyond its previous confirmed find. Size measurements for the specimens of *P. aurorae* are given in Table III.

Cidaroid epifauna

No epifauna were found on any of the species of irregular echinoids, or regular echinoids of the family Echinidae, at any of the sites or depths they were found. Most cidaroid echinoids had epifauna, mainly on their large primary spines, but also elsewhere. These cidaroid echinoids had considerable biodiversity associated with them, including eight phyla of animals as well Foraminifera and foliculinid protists (Table IV). Of the 51 faunal species (representing 10 classes) found on cidaroids all but seven were identified to genus level and most to species. By far the most rich epifaunal taxon was the Phylum Bryozoa, Class Gymnolaemata and the least the ascidians just represented by one species on one echinoid individual. Bryozoans and foraminiferans were the only taxa present as epifauna on every cidaroid species and recorded from every site.

The most colonized individual was an *Austrocidaris* cf. *spinulosa* from the Falkland Trough, which had 16 macrofaunal species attached. This species had the richest epifauna both in terms of average (6.5 ± 1.4 species) per individual and in total (Table IV). Meaningful comparisons of richness between cidaroid species, sites and depths were difficult because of such unequal sample sizes. ANOVA revealed no significant differences between echinoid species or sites ($F_{4,3} < 2.4$, $P > 0.056$). There were, however, significant differences between the sample depths ($F_2 = 27.8$, $P > 0.001$). The shallowest sample depths (160–200 m) were the richest with $4.89 (\pm 0.48, n = 38)$ epifaunal species per individual compared to $0.79 (\pm 0.19, n = 25)$ at 500 m and $0.43 (\pm 0.3, n = 7)$ at 1000 m. Thus there was an order of magnitude decrease in epifaunal richness from the shallow continental shelf to the continental slope.

Discussion

What we know about the sea floor of the Southern Ocean suggests that the macrofauna there is rich, can be abundant and much of it lives nowhere else (Arntz *et al.* 1994, 1997, Brandt *et al.* 2007a). In the shallows, the depth for which we know by far the most, echinoids are typically very abundant and ecologically important, not dissimilar to elsewhere in the world (Andrew *et al.* 2002, Jacob *et al.* 2003). Unlike elsewhere at most shallow localities around Antarctica this abundance is represented by the same single species. However, 74 echinoid species are known from the Southern Ocean (David *et al.* 2005a) of which we found nearly a third in 38 trawl samples or 50 500 m² within a small region, the Scotia Arc. The single species so dominant in abundance in the shallows and in the scientific literature, *Sterechinus neumayeri*, was found in just a single shelf sample. Few if any epibiotic species have ever been reported associated with *S. neumayeri*, so in the shallows echinoids are neither species rich nor harbourers of richness. The current study shows that the shelves around the Scotia Arc are both rich in species numbers of echinoids and their associated fauna but also that unlike the shallows they rarely dominate there.

What does echinoid distribution tell us about Southern Ocean benthos?

Echinoids are typically large, obvious and fairly easily identifiable animals for which a comprehensive database and identification guide to Southern Ocean species has been established (David *et al.* 2005a). There can be few taxa that will better reveal how well we know the Southern Ocean fauna. At a family level our findings were as might be expected. Most Antarctic echinoid species known are representatives of two dominant families, the Schizasteridae (22 species known) and Cidaroidae (15 species known) (David *et al.* 2005a). So it was in our

Scotia Arc shelf samples, these two families being represented by nine species each. The Echinidae, typically the most abundant but not species-rich, Antarctic family dominated the total numbers of specimens but were represented by just three species.

The current study of continental shelf and slope depths found 23 species at seven geographical localities. None of the 23 species we found were new to science - all were clearly identifiable as known species. At the next scale down, the number of echinoid species found represent a substantial proportion of the total. As 14 species have previously only been reported much deeper than we sampled (Brandt *et al.* 2007a), the 23 samples we report here comprise more than 38% of the known shelf and slope echinoids we could have expected to find. Either the Scotia Arc is disproportionately rich or disproportionably well sampled or both. Evidence of other scientific cruise paths and studies of other taxa suggests the Scotia Arc is both amongst the best studied of Antarctic regions and also very rich in species (e.g. Tatián *et al.* 2005, Ramos-Esplà *et al.* 2005, Hilbig *et al.* 2006, Linse *et al.* 2006b, Clarke *et al.* 2007, Primo & Vazquez 2007, Barnes & Griffiths 2008). At a finer scale, for many of the echinoid species we found, the localities, depths or sizes were new. For eight (~35%) of these, this was the first record of the species in the areas we found them in - the next nearest localities where they had previously been found were hundreds to thousands of kilometres away. Three species were found in shallower water than previously reported and four at larger sizes than previously known. Thus status of the echinoid species we found was changed by this study despite our sample protocol taking only single samples at each depth, focussing on the most sampled depth range, in one of the more sampled regions and the taxon being one of the most obvious and well known. In contrast to the Scotia Arc, sampling less well-known regions, such as the Amundsen Sea, should almost certainly increase known geographic and bathymetric ranges as well as unearthing new species.

Only two (28.6%) of the nine families but 27 (54%) of the 50 species known to occur within the Scotia Arc were not found by our sampling regime. Considering the small size of our sample areas and lack of replicates at each depth this very high 'find rate' suggests echinoid species are both fairly common and ubiquitous within the areas in which they occur. This certainly contrasts with patterns shown by some other taxa (e.g. isopod crustaceans, which appear to be highly patchy: equivalent sampling would only capture a tiny proportion of species at a given locality (Kaiser *et al.* 2007)). These two taxa seem to represent examples of opposite extremes of distribution, but we suggest that it is the echinoids which are unusual. Scientific sampling expeditions around the Scotia Arc have generally found both low proportions of e.g. ascidians, bryozoans, polychaetes, molluscs or other taxa known to occur in an

area and often new species of each (Ramos 1999, Arntz & Brey 2003, López-Fe 2005, Linse 2008).

Southern Ocean biogeography

Despite being one of the less speciose classes in Antarctica (Clarke & Johnston 2003), investigations of echinoid distribution can be particularly useful at elucidating Southern Ocean biogeography. Ease of identification makes literature data more reliable, most of their reproductive patterns are known, their fossil record is relatively (for the Southern Ocean) good and it is unlikely many new species will be found. Because the reproductive strategies of most Antarctic echinoids are known (Poulin *et al.* 2002, Pearse & Lockhart 2004, David *et al.* 2005a), distributions can be linked to apparent dispersal ability and thus how marine habitats in Antarctic have been colonized. The opportunity for a locality to be colonized and its subsequent diversity is dependent on geographic isolation and geological age of the locality. A strong fossil record, such as in the echinoids (Hotchkiss 1982, Néraudau *et al.* 2000), is particularly important around Antarctica where there have been massive oceanographic and climatic changes (e.g. Barrett 2001, Matsumoto *et al.* 2001, Mackensen 2004, Livermore *et al.* 2004, 2007, Maldonado *et al.* 2006) but there are poor preservation conditions. The current knowledge in Antarctic echinoid biogeography is summarized in David *et al.* (2005a, 2005b) and is publicly available in the SCAR MarBIN database (www.scar-marbin.be). Of the nine echinoid species for which the current study extends the known ranges, four are noteworthy (Fig. 5). With the exception of *Abatus curvidens*, all seem to be widely distributed around the Southern Ocean, supporting an old notion of Antarctic species being circumpolar (Hedgpeth 1969, Clarke & Johnston 2003). Echinoids are probably now one of the best examples of this concept, which has not proved so true in other taxa examined in detail (see Peña Cantero 2004, Allcock 2005, Collins & Rodhouse 2006, Linse *et al.* 2006b, Barnes & Griffiths 2008).

Of the species where we extended the ranges, only *Tripylaster philippi* occurs north and south of the Polar Front. Geographic distribution ranges crossing the Polar Front are known for a further 23 echinoids species, especially for deep sea species of the families Pourtalesidae and Urechinidae. Of shelf species, six species of Schizasteridae, five species of Cidaridae, three species of Echinidae and the arbaciid *Arbacia dufresnii* (Blainville, 1825) show cross-Polar Front distributions. Previously all records of *T. philippi* were Magellan or sub-Antarctic but our findings make it clear that it is a high-Antarctic species as well. The echinoids represent one of the best taxa to establish fairly reliable current range estimates and thus monitor Antarctic marine biological responses to climate change. Elsewhere in the world range extensions and

distributional changes have been one of the most obvious signals of regional warming (Walther *et al.* 2002). The Scotia Arc is both a centre for warming (Quale *et al.* 2002, Convey 2006) and the only shelf/slope link of the Southern Ocean to areas north of the Polar Front; this makes it the obvious place to look for organismal changes and invasions.

With one exception all new records we found were on the shelves of the South Shetland and South Orkney archipelagos. This is surprising as these islands are amongst the best-sampled areas in the Southern Ocean (e.g. Ramos 1999, Arntz & Brey 2003, Arntz *et al.* 2005b). In the Southern Ocean only in the Ross Sea has a similar intensity of sampling been reported at species level (Chiantore *et al.* 2006, De Domenico *et al.* 2006). The only echinoid we found on the slopes of the geologically young, isolated island of Southern Thule, South Sandwich Islands, was the deep-water species *P. aurorae*. *A priori* our expectation was that any echinoids at such a location would be those either with planktotrophic larvae (i.e. wide and fast dispersers) or deeper species colonizing up the slope from the surrounding abyssal plains. Our finding of *P. aurorae*, only the third confirmed record for this species, is interesting as its previously confirmed closest location was thousands of kilometres away in the Davis Sea.

Bathymetry and Antarctic benthos

The current study reports 19 trawls sampled at both shelf and slope depths. However the area sampled was 19.631 m² from 160–500 m compared with 30.870 m² at 1000–1500 m. Whilst the shelf samples yielded 19 species the slope samples, despite the greater area, contained just four. The greater supply of organic matter to the shelf makes such a result unsurprising, especially considering echinoids are often primary consumers, but also grazing generalists and deposit feeders (De Ridder & Lawrence 1982). However, just because each species is more abundant, and therefore more likely to be sampled on the shelf does not necessarily mean the shelves are richer in echinoids. It seems likely that with increasing depth proportionally greater areas need to be sampled to reach asymptote. This is supported by the fact that we found a smaller proportion of the echinoid species known to live below 1000 m depth than the proportion of those known to live on the shelf despite sampling 64% more of the deeper area. Antarctic benthos is known to be more eurybathic than fauna at most other locations (Brey *et al.* 1996). This varies between groups (Hilbig *et al.* 2006, Kaiser & Brandt 2007). The echinoid species reported here are quite eurybathic, their mean depth range being 1241 m (\pm 245 m) and only one of these has a known depth range of < 500 m. All but *Aporocidaris eltaniana* occur on the continental shelf yet nearly all these echinoid species occur deeper than 750 m. That the current study only found three incidences of species occurring outside previously known depth ranges suggests that the

pattern of echinoid bathymetric occurrence is probably fairly robust.

Size and biomass

As with bathymetry, the state of knowledge on maximum sizes in Antarctic echinoids seems to be fairly good. Our measurements of echinoid specimens generally lay within the size ranges reported by Jacob (2001) and David *et al.* (2005a). Antarctic echinoids may grow very slowly (Brockington 2001), especially at larger size/age, so increases in 8–9 mm of test diameter that we report for *Ctenocidaris spinosa*, *A. rostratus* and *B. chesheri* may have significant implications for their lifespan. It is likely that even this small increase in diameter of nearly 1 cm might mean these species live decades more than previously thought. However, we appreciate that site and food availability differences could account for significant differences in growth characteristics (David & Laurin 1991, Mespouhlé & David 1992).

Echinoids can often be the major component of shelf biomass and representatives of the *Echinidae* can fill ROV film of benthos or trawls from Antarctic shelves (e.g. Barry *et al.* 2003, Cranmer *et al.* 2003). However, of the 38 trawls in the current study, only one was dominated by echinoids suggesting that our view of them as a dominant group based on super-abundance in the shallows is rarely the case at depth. Most regular echinoids showed straightforward increases in mass with increasing test length, though strangely *C. spinosa* showed negligible increase in mass with length (Fig. 2). Echinoid contribution to biomass can be reported as simple wet mass, but we found this to be highly variable between species. Relationships between dry mass and ash free dry mass were more robust but whilst cidaroid species were typically ~17% tissue mass, irregular species varied from 17.7% (*A. curvidens*) to 11.2% and 8.9% (*A. ingens* and *T. phillipi* respectively). It is clear both that meaningful estimates of echinoid contributions to biomass need to involve identifications to species level and that irregular species show considerable intraspecific variability.

Echinoid associated biodiversity

In tropical and temperate seas, echinoids are often associated with changing levels of biodiversity through their grazing activities. Keystone roles in mediating biodiversity (see Elner & Vadas 1990) are unlikely in the Antarctic as most species occur below the depth of macroalgae and ice scour is pivotal in the shallows (see David *et al.* 2005a, Barnes & Conlan 2007). However, whilst most echinoids, such as *Echinidae* or *Schizasteridae*, are rarely fouled by epibionts, the *Cidaroid* families carry a variety of taxa (Jacob 2001, David *et al.* 2003, Hétériér *et al.* 2004, Massin & Hétériér 2004). A variety of animal externa from pycnogonan legs

to brachiopod shells can be important, particularly with increasing depth because of the rarity of hard surfaces (Barnes & Clarke 1995). The biodiversity associated with our study cidaroid species is greater (at all taxonomic levels) known to the authors, than has ever been previously described on any other Antarctic organism externa. Such cidaroid associated biodiversity declined considerably with depth but is probably quite important at all depths. Firstly, the 70 cidaroids examined represent only a relatively small amount of surface area, yet had 10 classes and 51 benthic species associated with it (Table IV). Representatives of up to eight phyla had been previously reported from a study of two species of Antarctic cidaroids, but were not identified beyond phylum level (Hétériér *et al.* 2004). Some of the associated species in the current study are otherwise very rare. For example *Escharoides torquata* found on *N. mortenseni* at Elephant Island had only previously been found at a single site at South Georgia (Hayward 1995). Secondly, there was little overlap in epibiota between different cidaroid specimens suggesting other specimens would contribute further to local biodiversity. Third, many of the species, which occurred as cidaroid epibiota, were not otherwise found in those trawls or even areas (BIOPEARL unpublished data). Many such species only or mostly occur as epibiota (Barnes & Clarke 1995). For trawls of the BIOPEARL cruise in which cidaroids were present, echinoid associated fauna was (on average) > 38% of the total number of species recorded, clearly a significant contribution to total biodiversity of a local area. In addition in a number of trawls the epibionts of cidaroids were a major proportion of all the sessile (and even total) species found. Finally most of the epibiota were sessile without planktotrophic larvae and thus with limited powers of dispersal. Being attached to mobile echinoids increases possibilities for dispersal and so colonization of this component of biodiversity.

In summary, this study provides results on the geographic distributions of echinoid species, including ranges extensions in nine species, on their test size and biomass relationships and on their associated epibiont biodiversity. Our data enhances the knowledge on biogeography and biodiversity patterns in the Antarctic benthos and shows the need for more, internationally co-operative research to establish a comprehensive picture of the biodiversity of shelf, slope and deep sea habitats of the Southern Ocean.

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