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David K. A. Barnes and Lloyd S. Peck

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Epibiota and attachment substrata of deep-water brachiopods from Antarctica and New Zealand

DAVID K. A. BARNES AND LLOYD S. PECK

British Antarctic Survey, High Cross, Madingley Road, Cambridge CB3 0ET, U.K.

SUMMARY

Prevalence (proportion of host organisms covered) and cover of encrusting epibiota were investigated for four Antarctic and two New Zealand species of deep-sea brachiopods. All epibiota was identified to the lowest possible taxonomic level, such that prevalence and dominance of each taxon could be assessed on different brachiopod species. Punctae had no detectable influence on fouling, whereas valve architecture and ornamentation were probably a major influence. Prevalence and percent cover of epibiota were found to decrease with depth (from 50–600 m) in the Antarctic terebratulid *Liothyrella uva*. A maximum of 5% epibiotic cover was recorded on the punctate terebratulids from beyond 160 m (*Liothyrella uva*, *Magellania fragilis* and *Magellania joubini* from Antarctica and *Neothyris lenticularis* from New Zealand). Epibiotic cover significantly increased with valve area to over 40% in the Antarctic inarticulate *Neocrania lecointei* and the New Zealand impunctate rynchonellid *Notosaria nigricans*. Bryozoans, foraminiferans and polychaetes were the most abundant colonizers, but there were also representatives present from seven other phyla. The epibiotic community structure of the terebratulids *Liothyrella uva*, *Magellania joubini* and *Neothyris lenticularis*, and the inarticulate *Neocrania lecointei* were broadly similar, suggesting a cosmopolitan nature to deep-sea brachiopod epibiota. The community on *Magellania fragilis* was notably different, in being almost entirely dominated by foraminiferans, but the reasons for this are unknown. Analyses of attachment substrata for the Antarctic terebratulid brachiopods indicated erect bryozoans were most commonly used, but that sponges, rocks and even echinoid spines were used. The substratum used by the majority of the New Zealand specimens was unknown, but this is possibly because *N. lenticularis* has been described as degenerating its attachment and becoming free-living with age.

1. INTRODUCTION

The influence of fouling epibiota on their substratum organism has been a topic of considerable scientific and commercial interest for a number of decades. Some research has indicated beneficial effects for the species colonized, such as camouflage in decapod crustaceans (McLay 1983; Maldonado & Uriz 1992). Most studies have, however, found only minor or occasionally detrimental effects, although in extreme cases fouling has lead to the death of the host organism (Barnes & Clarke 1995). The obvious importance of this topic to shipping and drilling installations, and the ease of access to tidal and immediately subtidal habitats has meant that studies have predominantly concentrated on shallow-water temperate environments, where competition for space is typically considered to be intense (Dayton 1971; Paine 1974; Jackson 1977; Thayer 1985; Vermeij 1987). In these conditions biological constructs, especially valves or exoskeletons, may be important as substrata for epifaunal colonizers. By contrast, in the deep sea, numbers of colonizers might be expected to be less, but the relative scarcity of hard substrata available for colonization (Gage & Tyler 1992; Arntz *et al.* 1994) could lead to similar, or even higher levels of importance to epifauna for biological surfaces.

Brachiopods have one of the most abundant and long-standing fossil records of any metazoan, with some taxa appearing to have been represented almost unchanged over the past 550 Ma since early Cambrian times. For large parts of Phanerozoic time they dominated benthic communities in near-shore and shelf environments. Because of this, over 97% of brachiopod species known occur only as fossils (Barnes 1984). They are present, however, in all of the seas of the world and can still dominate assemblages locally (Brey *et al.* 1995). Despite this, living species are little known and rarely studied by biologists. This is partly because they are common only in cryptic habitats or in geographically isolated areas such as fiords or Antarctica (Curry *et al.* 1992). Much of the current knowledge of brachiopod biology has, therefore, come from work by palaeontologists studying living specimens to obtain data relevant to evolutionary and palaeontological questions (e.g. Steele-Petrovic 1975; Thayer 1979, 1985; Thayer & Allmon 1990), rather than by zoologists. Biological investigations of living brachiopods have also been restricted predominantly to a few sites, such as the west coast of north America (Long 1964; LaBarbera 1981, 1985), the Antarctic (Peck 1989; Brey *et al.* 1995), or New Zealand (Neall 1970; Doherty 1979; Lee 1990).

In Antarctica, sessile suspension feeders are highly abundant and often dominate benthic assemblages from the sublittoral through to deep-water environ-

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ments (Bullivant 1961, 1967; Knox 1970; Winston & Heimberg 1988; Galéron *et al.* 1992). The lophophorate phyla, brachiopods and bryozoans, may be more abundant and diverse here than in any other marine environment (Foster 1974; Winston & Heimberg 1988; Barnes 1995), and in certain specific locations, for example caves, single brachiopod species may dominate assemblages (Brey *et al.* 1995; D. K. A. Barnes & L. S. Peck, personal observations). Antarctic species which are abundant and accessible for *in situ* and laboratory study, such as the shallow-water terebratulid *Liothyrella uva* Broderip have been the focus of unusually detailed investigations into metabolism (Peck *et al.* 1986, 1987), predation potential (McClintock *et al.* 1993; Peck 1993), growth (L. S. Peck & T. Brey, unpublished data) and epifaunal communities (Barnes & Clarke 1995).

New Zealand is one of the few areas where articulate brachiopods occur commonly in intertidal and shallow-water subtidal habitats. Because of this, a wide range of species have been investigated (see e.g. Rudwick 1962; Neall 1970; Doherty 1979; Richardson 1981; Dawson 1990*a*). Habitat (sea-floor type) has been shown to be important for overall brachiopod distributions, and microsubstratum (attachment surface) to individual survival (Lee 1990). Lee also indicated that hard biological substrata, including coral skeletons and oyster, mussel and gastropod valves, may be important attachment sites for brachiopods in the shelf sediments around New Zealand. A number of New Zealand brachiopods have also been reported as attachment substrata for epifaunal suspension feeding organisms, including other brachiopods (Rudwick 1962, 1965; Doherty 1979; Lee 1990).

The aims of this study were to describe and contrast the epibiota and attachment substrata of six deep-water brachiopods from Antarctica and New Zealand. Several populations of *Liothyrella uva* were examined to determine how epibiotic communities varied in prevalence, cover and diversity with depth. The abundance and dominance of a range of epibiotic taxa are investigated on articulate and inarticulate, punctate and impunctate and ribbed and unribbed brachiopods. The substrata to which brachiopods were attached were also identified and quantified, to examine their importance to deep-water brachiopod abundance and distribution.

2. MATERIALS AND METHODS: STUDY SITE AND SPECIES

Brachiopods were collected from one site in New Zealand and several sites in the Weddell Sea, Antarctica (figure 1). The site in New Zealand was east of Tiaroa Head (45° 50′ S, 171° 50′ E) on the east coast of South Island and is described in detail in Peck (1993). The punctate *Neothyris lenticularis* Deshayes ($n = 51$) and the impuctate *Notosaria nigricans* Sowerby ($n = 41$) were dredged from between 160 and 180 m depth, and preserved in alcohol for examination in the U.K.

The collections made in Antarctica came from several sites in the Weddell Sea near 69° 57′ S, 11° 49′ E and one site close to Signy Island at 60° 43′ S, 45° 36′ W (figure 1). Specimens were collected in 1986, 1988 and 1991 from the RV Polarstern using an Agassiz trawl. The brachiopod species present in the samples were identified from Foster (1974). The punctate inarticulate brachiopod *Neocrania lecointei* Joubin (30 specimens) was found at 360 m. The punctate articulate brachiopods *Magellania fragilis* Smith (359 specimens) and *Magellania joubini* Blochmann (66 specimens) were found at 210–220 m depth and *Liothyrella uva* (104 specimens) at depths between 50 and 600 m. All brachiopods were again preserved in alcohol for examination in the U.K.

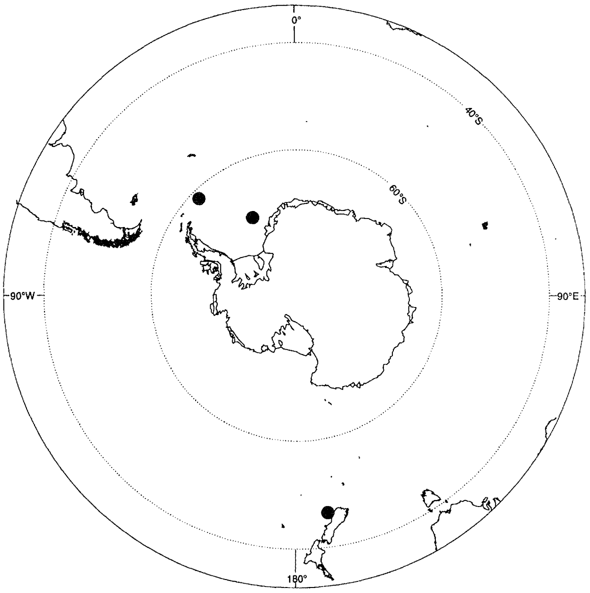

Figure 1. Map showing collection point of samples in New Zealand and Antarctica.

The length, width and height of each brachiopod was measured to the nearest 0.1 mm using vernier calipers. Upper and lower valve surface areas, as well as the area occupied by epibiota, were measured using a non-elastic net marked in a grid of square centimetres following the protocol of Barnes & Clarke (1995). Only the upper valves of the *Neocrania lecointei* were available for measurement as the lower valves are cemented to the substratum (Foster 1974). The valves of *Notosaria nigricans* were ribbed and therfore have a larger surface area than those of the other species in this study with smooth valves. There was clearly some error in the measurement of available surface area in *N. nigricans*, however, as the ribbing has low relief this error is minor. All epibiota was examined using a binocular microscope and identified to the lowest possible taxonomic level. The substratum which each individual brachiopod used for attachment was also identified, where possible.

The sample populations of each brachiopod species were separated into four approximately equally represented size classes. This allowed comparisons of epibiota prevalence and mean coverage with valve surface area, and in addition enabled meaningful comparisons of the different species to be made despite size differences.

3. RESULTS

(*a*) *Epibiota on* Liothyrella uva

The prevalence of epibiota (the proportion of valves with epibiota present) on *Liothyrella uva* decreased with depth from 67% at 50–100 m to 42% at 300–600 m. This trend continues into shallow water as shown by the inclusion of data from Barnes & Clarke (1995) for a 0–50 m population (figure 2*a*). The percentage valve area covered by epibiota also decreased with depth, although too few valves were available to assess whether there was a significant difference between populations at 100–300 m and 300–600 m (figure 2*b*). Although *L. uva* showed considerable overlap in the extent of cover by epibiota in the smaller size classes, in the largest size class (adults; see Peck & Holmes 1989) there was a tenfold difference between the shallowest and the deepest populations examined. In addition to the decreased magnitude, the variation in percent cover of brachiopods from 100–300 m and 300–600 m was also considerably lower than those shallower than 100 m (figure 2*b*). There was no significant difference in cover between the upper and lower valves in *L. uva* ($t = 0.07$, $p = 0.95$, $n = 104$).

Bryozoans, polychaetes and foraminiferans were the major colonizers in terms of both numbers and area occupied by epibiota (figure 3). From shallow water to 100 m depth, most *Liothyrella uva* with epibiota were colonized by bryozoans and polychaetes, whereas below 100 m, the epibiota were dominated by foraminifera. The apparent increase in foraminifera was largely because of greatly decreased bryozoan and polychaete abundance, rather than any significant increase in absolute foraminiferan abundance. The bryozoan component of this community constituted several unidentified cyclostomatid and five cheilostomatid species, the most abundant of which were *Celleporella antarctica* (Powell) and *Celleporella bougainvillei* (d'Orbigny). The other less frequently occurring epibiotic taxa were demosponges and juvenile *Liothyrella uva*. Table 1 lists the epibiota found on *L. uva* and the other three Antarctic brachiopod species investigated. The low degree of colonization on valves meant colonists rarely met and thus few interactions were observed within communities of epibiota.

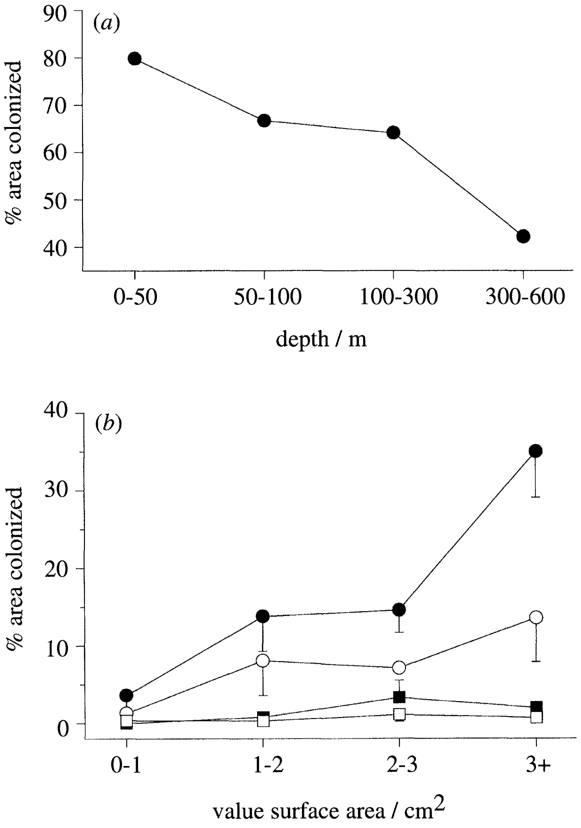

Figure 2.(*a*) Prevalence of epibiota on valves of *Liothyrella uva* with depth. Data point labelled 0–50 m was from samples collected at 12 and 25 m in Barnes & Clarke 1995 pp. 691. (*b*) Percent cover by epibiota of *Liothyrella uva* with depth and valve surface area. Data are shown as mean with standard error and plotted separately for the depth horizons 0–50 m (filled circles), 50–100 m (open circles), 100–300 m (filled squares) and 300–600 m (open squares).

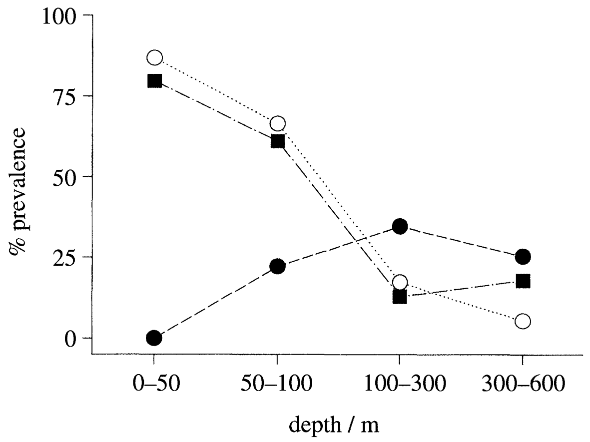

Figure 3. Prevalence of the three most important epibiotic taxa on *Liothyrella uva* with depth. The taxa are foraminiferans (filled circles), bryozoans (filled squares) and polychaetes (open circles).

(*b*) *Epibiota of other Antarctic brachiopods*

The punctate articulates *Magellania fragilis* and *Magellania joubini* are superficially similar in appearance to *Liothyrella uva*, although they do have much thinner valves, particularly *M. fragilis*. The prevalence of epibiota on both species was very high (> 99% on *M. fragilis* and 91% on *M. joubini*). The inarticulate species *Neocrania lecointei* had epibiota on 90% of the valves examined. In contrast to the high levels of epibiota prevalence, the mean percent cover of valves in both *M. fragilis* and *M. joubini* was below 5% (figure 4). Thus in the articulate species nearly all specimens were colonized, but by only a few epifauna. The variation in percent cover was also very low. With the exception of the smallest size class, the percent cover of *N. lecointei* valves was significantly higher than either *M. fragilis* and *M. joubini*, and in the largest size class higher than *Liothyrella uva*. The between-individual variation in *N. lecointei* was high but this may at least be partly due to the lower sample size compared to the other Antarctic species examined. There were no significant differences between the cover of upper and

Table 1. *Epibiota occurring on four deep-water Antarctic brachiopods*

(Epibiotic representatives from each phylum were identified to the lowest taxonomic level possible.)

	brachiopod species			
epibiota	*M. fragilis*	*M. joubini*	*L. uva*	*N. lecointei*
Annelida	serpulid spirorbinid	serpulid spirorbinid	serpulid spirorbinid	serpulid
Brachiopod	*Magellania fragilis*		*Liothyrella uva*	
Bryozoa	cheilostomatida *Dendroperistomata* *Fenestrulina* sp. *Lacerna eatoni* *Micropora brevissma* *Microporella stenoporta* cyclostomatida unknown sp.	cheilostomatida *Amphiblestrum familiaris* *Arachnopusia inchoata* *Cabarea darwinii* *Camptoplites bicornis* *Ellisina antarctica* *Lacerna eatoni* *Micropora brevissima* *Microporella stenoporta*	cheilostomatida *Amphiblestrum familiaris* *Arachnopusia inchoata* *Celleporella antarctica* *Celleporella bougainvillei* *Micropora brevissima* cyclostomatida *unknown sp.*	cheilostomatida *Arachnopusia inchoata* *Ellisina antarctica* *Escharoides tridens* *Kymella polaris* *Smittina* sp. cyclostomatida unknown sp.
Ciliophora		heterotrichid		
Cnidaria	hydroid	hydroid		hydroid
Porifera		*demospongiae*	demospongiae	demospongiae
Sarcodina	foraminifera	foraminifera	foraminifera	foraminifera
Urochordata	*Bathypera splendens*			

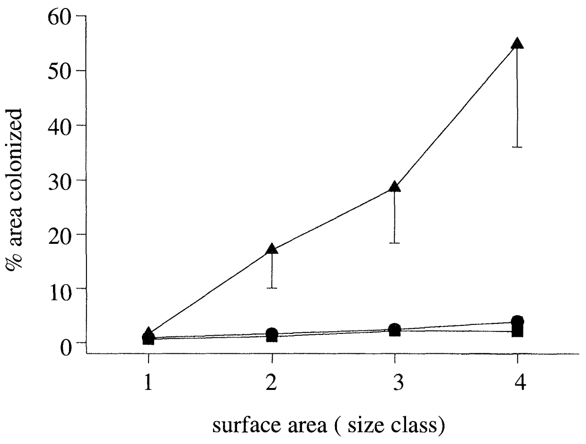

Figure 4. Relation between valve area of three Antarctic brachiopods covered by epibiota and valve surface area, separated into separate size class (see text). The brachiopods are *Neocrania lecointei* (filled triangle) (size class 1 (0–1 cm^2), size class 2 (1–2 cm^2) size class 3 (2–3 cm^2), size class 4 (> 3 cm^2)), *Magellania joubini* (filled circles) (size class 1 (0–1.7 cm^2), size class 2 (1.7–2.7 cm^2), size class 3 (2.7–3.7 cm^2), size class 4 (> 3.7 cm^2)), *Magellania fragilis* (filled squares) [size class 1 (0–3 cm^2), size class 2 (3–6 cm^2), size class 3 (6–9 cm^2), size class 4 (> 9 cm^2)).

lower valves of either *M. fragilis* (Students $t = 1.1, p = 0.27, n = 359$) or *M. joubini* ($t = 0.17, p = 0.87, n = 66$). The permanent attachment of the lower valve to the substratum in *N. lecointei* leads to obvious differences in colonization between upper and lower valves, thus statistical analyses are redundant.

Virtually all epibiota of *Magellania fragilis*, *Magellania joubini* and *Neocrania lecointei* were encrusting taxa (including the hydroid species present), although a few erect bryozoans (*Cabarea darwini* (Busk), *Camptoplites lewaldii* (Kluge) and *Kymella polaris* (Waters)) occurred infrequently (table 1). *Magellania fragilis* and *M. joubini* have been described as having apparently similar superficial external anatomy, habitat, total epibiota prevalence, percent colonization of valves and diversity of epibiotic taxa. The community structure of the epibiota on the valves of these two species was, however, totally different (figure 5). Bryozoans, foraminiferans and polychaetes were respectively the most common colonizing agents on valves of *M. joubini* and *N. lecointei*. Foraminiferans colonized 99% of the valves of *M. fragilis*, whereas no other taxon colonized more than 16% of valves of this species. This is the main reason that epibiotic communities on *M. fragilis* have an almost singular taxonomic pattern of dominance (figure 6). The epibiota of *M. fragilis* also differed from that of other Antarctic brachiopods studied in the lack of any sponges. Bryozoans, where they occurred, were usually the dominant space occupiers on valves of *M. joubini* and *N. lecointei* and thus dominated the majority of epibiota of these two species. Sponges and tunicates, though comparatively rare, similarly tended to dominate assemblages, when present, through superior overgrowth capabilities and spreading growth patterns. Foraminifera, by comparison, dominated relatively few epibiotic communities despite being the second-most abundant taxon.

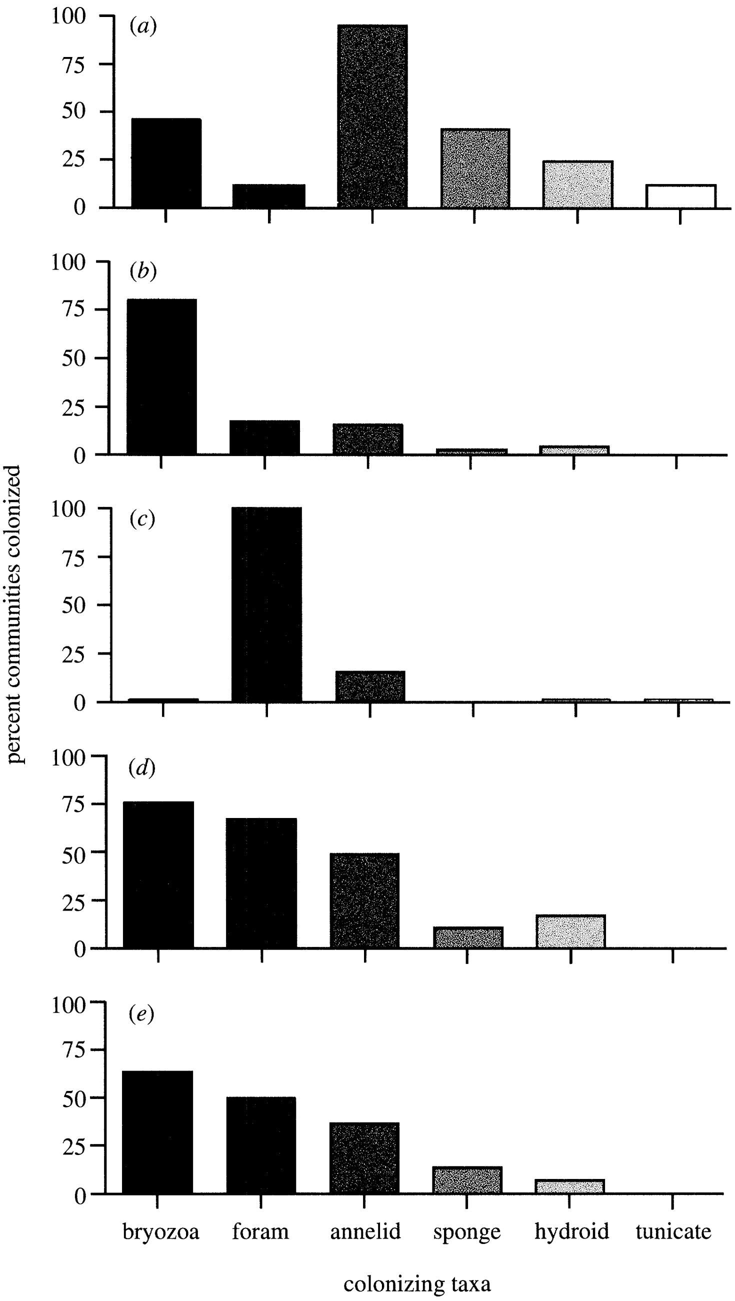

Figure 5. Prevalence of major epibiotic taxa on five species of brachiopods. Histograms denote the proportion of valves of each brachiopod colonized by each epifaunal taxon. (*a*) *N. nigricans*; (*b*) *N. lenticularis*; (*c*) *M. fragilis*; (*d*) *M. joubini*; (*e*) *N. lecointei*.

(*c*) *Epibiota of New Zealand brachiopods*

The punctate *Neothyris lenticularis* and impunctate *Notosaria nigricans* have overlapping habitats. They were collected at the same site and *N. lenticularis* individuals were found on valves of *N. nigricans*. Both species showed a considerable degree of clumping, although the sample size was too small to investigate any possible influence of this clumping on epibiota or coverage (see Barnes & Clarke 1995). The two species studied, *N. lenticularis* a terebratulid and *N. nigricans* a rhynchonellid, differ considerably in external valve morphology. The two valves of *Notosaria nigricans* are shaped differently, are ribbed, and are without punctae. In contrast the upper and lower valves of *N. lenticularis* are of similar shape, unribbed, punctate and may attain a surface area several times greater than *N. nigricans*. It is not therefore particularly surprising that the prevalence of epibiota on the valves of these two species was considerably different (80.4% in *N. lenticularis* and 100% in *N. nigricans*). However, the mean percent cover of *N. lenticularis* was significantly lower (by a factor of about 20) than *N. nigricans* in all size classes (figure 7). There was no significant difference in percent cover between the upper and lower valves of *N. lenticularis* ($t = 1.91$, $p = 0.06$, $n = 51$), but epibiotic cover on the upper valves of *N. nigricans* was higher than lower valves ($t = 2.26$, $p = 0.03$, $n = 41$).

The diversity of epibiota on *Notosaria nigricans* was

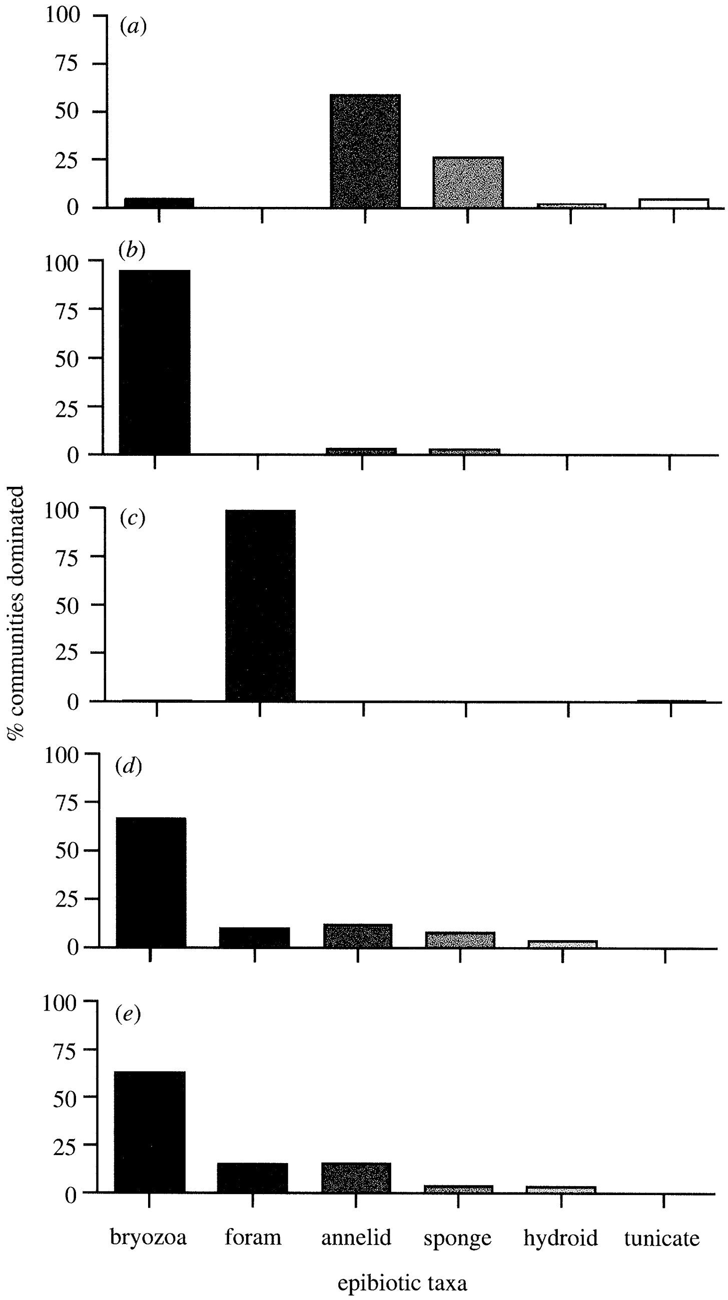

Figure 6. Proportion of total number of epibiotic communities dominated (by area) by each taxon for each species of brachiopod. (*a*) *N. nigricans*; (*b*) *N. lenticularis*; (*c*) *M. fragilis*; (*d*) *M. joubini*; (*e*) *N. lecointei*.

the richest of any species studied, being the only deep-water brachiopod with crustaceans and entoprocts amongst its colonists, in addition to more typical fouling taxa (table 2). The epibiotic taxa present on *Neothyris lenticularis* were similar to those found on the Antarctic articulates. Bryozoans, foraminiferans, hydroids, sponges and tunicates were all common on *N. nigricans*, although polychaetes were by far the most abundant epibionts numerically (figure 5). Polychaetes and sponges dominated (greatest space occupiers) most of the epibiotic communities on *N. nigricans* (figure 6). Generally polychaetes dominated the early stages of community development (i.e. on small specimens) and sponges dominated more developed communities (by overgrowth of other epibionts) usually those on larger or adult brachiopods. Bryozoans were the only common epibionts of *N. lenticularis* and consequently also completely dominated the community in terms of area occupied.

(*d*) *Substrata used for attachment*

Rigid erect bryozoans of the genera *Melicerita*, *Cellarinella* and *Cellaria* were the principle source of attachment surface for the three Antarctic terebratulid brachiopods; *Liothyrella uva*, *Magellania fragilis* and *Magellania joubini* (table 3). Interestingly individuals of all three species, albeit rarely, were found attached to sponges and 2 specimens of *M. fragilis* were attached to echinoid spines. Relatively low proportions of each sample had pedicles broken or disattached to give unknown results. In contrast 50% of the attachment

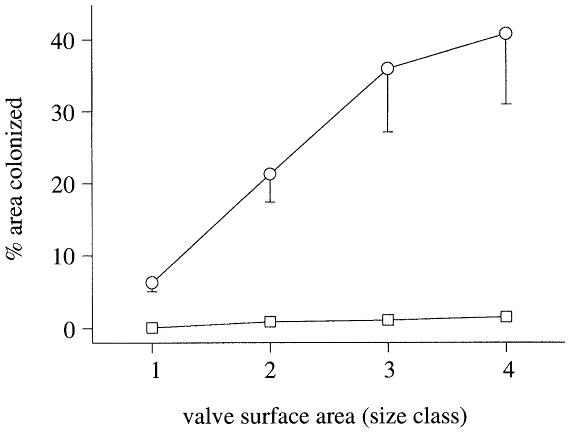

Figure 7. Relation between valve area of two New Zealand brachiopods covered by epibiota and valve surface area size class (see text). The brachiopods are *Notosaria nigricans* (open circle) (size class 1 (0–1.1 cm^2), size class 2 (1.1–2.2 cm^2), size class 3 (2.2–3.3 cm^2), size class 4 (> 3.3 cm^2)) and *Neothyris lenticularis* (open squares) (size class 1 (0–2 cm^2), size class 2 (2–4 cm^2), size class 3 (4–6 cm^2), size class 4 (> 6 cm^2)).

Table 2. *Epibiota occurring on two deep-water New Zealand brachiopods*

(Epibiotic representatives from each phylum were identified to the lowest taxonomic level possible.)

	brachiopod species	
epibiota	*N. nigricans*	*N. lenticularis*
Annelida	serpulid spirorbinid	serpulid spirorbinid
Brachiopoda	*Neothyris lenticularis* *Notosaria nigricans*	*Neothyris lenticularis*
Bryozoa	cheilostomatida *Chaperia acanthina* *Escharoides angela* *Fenestrulina disjuncta* *Scrupocellaria ornithorhynchus* cyclostomatida *Disporella* sp.	cheilostomatida *Arachnopusia unicornis* *Chorizopora brongniartii* *Microporella agonistes* cyclostomatida *Annectocyma* sp. *Disporella* sp.
Ciliophora		heterotrichid
Cnidaria	hydroid	hydroid
Crustacea	Cirripedia *Notobalanus vestitus*	
Entoprocta	*Barentsia* sp.	
Porifera	demonspongiae	demonspongiae
Sarcodina	foraminifera *Aceruulina inhaerens*	foraminifera
Urochordata	tunicate	

substrata for the two New Zealand species were unknown, which may reflect sampling procedures (although it is unlikely). Conspecific settlement on other brachiopods, bryozoans and small pebbles accounted for most of the known substrata, but both species have been described as progressively reducing attachment until becoming free-living as adults (Neall 1970; Richardson 1981).

4. DISCUSSION

Many Recent (and fossil) brachiopods have been reported to have associated epibiotic communities (Rudwick 1965; Doherty 1979; Hammond 1984; Thayer & Allmon 1990; Cuffey *et al.* 1995). They are hard-valved, sessile, relatively long-lived (see James *et al.* 1992), and sometimes locally superabundant (Foster 1974; Brey *et al.* 1995). Brachiopods may, therefore, represent an ideal hard substratum for many encrusting organisms. This is likely in the sublittoral of Antarctica, northwest America and in Scandinavian and New Zealand fiords where competition for space is intense and brachiopods are both diverse and abundant. Brachiopods might also be of particular importance to encrusting deep-water biota, where hard substratum is comparatively rare and brachiopods may dominate assemblages as well as reaching substantial ages (James *et al.* 1992; Brey *et al.* 1995). This would provide a long-term temporally and spatially stable habitat for encrusting organisms.

The marine environment around New Zealand has long been recognized for its importance to Recent brachiopod biology. Dawson (1990*a*, *b*) describes 32 resident species, some of which may be found intertidally. Epibiota has been observed or described from a number of shallow-water New Zealand brachiopods, e.g. *Notosaria nigricans* (Percival 1960; Lee 1978), *Calloria inconspicua* (Rudwick 1962; Doherty 1979), *Neothyris lenticularis* (Neall 1970), and *Liothyrella neozelandica* (Grange *et al.* 1981). A wide variety of fauna, both encrusting (foraminifera, sponges, hydroids, polychaetes, ascidians and barnacles) and mobile (nemerteans, ophiuroids, pycnogonids, mites and various crustaceans), have been observed on shallow-water *N. nigricans* (Percival 1960; Lee 1978). Associated fauna living with deep-water (200 m) specimens of *N. nigricans* has been observed in both fossil (Gage 1957) and living (Dell 1954) assemblages, though the epibiota was undescribed.

The epibiotic assemblages of the brachiopods examined here showed many similarities across sites although there were also important individual and species differences. *Notosaria nigricans* had the most diverse epibiotic communities of any of the deep-water specimens examined, comprising sessile representatives from nine phyla. Bryozoans were one of the most abundant colonizers, as also found in a study of 200 dead specimens by Lee (1978). In no instances did encrusting epifauna completely overgrow either young or adult *N. nigricans*, whereas Barnes & Clarke (1995) found such overgrowth as a possible cause of mortality in shallow-water *Liothyrella uva*. Sponges were found overgrowing the anterior commissure of dead valves of *N. nigricans* (Lee 1978), however, it is uncertain whether this growth occurred either *pre* or *post mortem*. The other New Zealand and Antarctic species supported slightly less diverse communities of epibiota consisting of representatives of between five and seven phyla. In contrast to the diverse epibiotic communities Barnes & Clarke (1995) found on shallow-water *L. uva* including 13 species of cheilostomatid bryozoans, the epibiota of deep-water *L. uva* was relatively

Table 3. *Attachment substrata of deep-water brachiopods from New Zealand and Antarctica*

(Data are expressed as percent of total specimens attached to each substratum.)

attachment substratum	brachiopod species *N. nigricans*	*N. lenticularis*	*M. fragilis*	*M. joubini*	*L. uva*
bryozoa	4.9	23.5	63.5	65.2	73
brachiopod	26.8	7.8	7.8	0	1
porifera	0	0	2.8	1.5	7
polychaete	2.4	0	0	1.5	0
echinoid	0	0	0.6	0	0
rock	9.8	9.8	10.9	4.5	2
unknown	56.1	58.8	14.5	27.3	17

impoverished, with just five cheilostomatid bryozoan species.

(*a*) *Punctae and valve architecture*

As with *Liothyrella uva* most other deep-water brachiopods had impoverished epibiota. In contrast, however, *Neocrania lecointei* was heavily encrusted. This is at least partly because it is an inarticulate, with one valve rigidly attached to a hard substratum. The upper valve of *N. lecointei* would present an easier surface for larval settlement. In addition, high levels of colonization could also be due to the proximity of rocky hard substrata, where epibiota are abundant. This differs from the terebratulids and rhynchonellid study species, which are not confined to rocks and may colonize unconsolidated substrata. Conversely *Neothyris lenticularis* has, in common with the other terebratulids in this study, valves which are smooth and of similar shape. The greatly dissimilar and ribbed upper and lower valves of *Notosaria nigricans* provide a surface which is hydrodynamically easier to settle and remain on. *N. nigricans* was the only articulate species to have significantly different degrees of epibiotic cover on its upper and lower valves. There are two likely explanations for upper valves being more heavily colonized. The clumping behaviour of *N. nigricans* probably makes the more hidden lower valve harder to colonize, and it's greater convexity probably facilitates the removal of epibiota by abrasion against substratum as the brachiopods rotate on their pedicles.

The data showing far greater colonization of valves of the impunctate *Notosaria nigricans* compared with *Neothyris lenticularis* could be taken as support for the idea that caeca deter epifauna (Owen & Williams 1969; Thayer 1975; Curry 1983). However, in Antarctica *Neocrania lecointei* was much more heavily colonized by epifauna than other deep-water brachiopods, and is punctate. The punctae of inarticulates, though, are very different in structure from articulates, and it could be argued that their functions differ. Barnes & Clarke (1995) often found shallow-water *Liothyrella uva* completely covered by epibiota, and there was some evidence that in a few cases brachiopods had been killed by overgrowing organisms. They also found that *L. uva* was more highly colonized than nearby pebbles with similar surface areas, and that some epifauna were specific to *L. uva* valves, producing a unique and diagnostic epifaunal community. Doherty (1979) found high colonization levels of valves of New Zealand brachiopods, and also found potentially detrimental effects to the hosts. These data indicate that there is no anti-fouling function for caeca, or that its effect is insignificant. The strong colonization seen in this study of the inarticulate *N. lecointei* and the impunctate *N. nigricans* is, therefore, probably due to valve architecture and ornamentation. The valve of *N. lecointei* is covered in pustules (*sensu* Foster 1974) and that of *N. nigricans* is highly ridged, whereas the other brachiopods here had smooth valves. The pustules and ridges would both serve to increase the thickness of the boundary layer of water flowing over the valves, possibly enhancing settlement. They would also provide protected microhabitats for newly settled epifauna. Despite sharing similar external anatomy, habitat, total epibiota prevalence, percent colonization of valves and range of epibiotic taxa, the epibiota of *Magellania fragilis* and *M. joubini* was completely different. The former was dominated by foraminiferans and the latter by bryozoans. Both are punctate and it seems unlikely that the difference in punctae density (56 mm^{-1} in *M. fragilis*, and 94 mm^{-1} in *M. joubini*: Foster 1974) could account for this. The lack of deterrant effect on epifauna by punctal is further enhanced by the data from *M. fragilis* and *M. joubini*. Given that epifauna are not deterred from settling on brachiopod valves, the strong decline in prevalence and percent cover with depth (figure 2*a*, *b*) must be due to other factors.

(*b*) *The influence of depth*

Prevalence of epibiota on *Liothyrella uva* decreased consistently from 80% at 50 m to 40% at 600 m. If punctae had a significant deterrent effect on epifauna the large decreases in colonization seen with depth in *L. uva* would also not occur. This trend has also been shown for shallow sublittoral populations of the same species at Signy Island (Barnes & Clarke 1995). The reduced epibiotic cover found on *L. uva* below 100 m removes any potential disadvantage to the brachiopod from overgrowth, and any advantage in camouflage from predators. Advantages from camouflage are, however, likely to be small because predation on brachiopods is low (James *et al.* 1992), possibly because of poor cost to benefit ratios for predators (Peck 1993) or the presence of chemical defences (McClintock *et al.* 1993). Identified predators of articulate brachiopods have also mainly been species using non-visual cues while hunting, such as gastropod molluscs and asteroids.

The structure of the associated epibiotic community changed with depth from one dominated by bryozoans within 100 m to one being chiefly foraminifera below 100 m. Overall percent cover and community structure of the epibiota of *L. uva* differ widely with depth. Combining this with the findings of Barnes & Clarke (1995), that epibiota of *L. uva* were not significantly different in major respects from similarly stable natural substrata, suggests the development and nature of epifaunal communities may be indicative of habitat depth. Epifauna on fossil brachiopods have been used recently to infer living and *post mortem* orientations. Clearly, from the data presented here, epifauna could also be used as indicators of palaeoenvironment depth with dominance by foraminiferans, for example, indicating deep-water sites.

(*c*) *Epibiotic community similarities across deep-water sites*

All the Antarctic terebratulids from similar depths had similar percentage cover. Thus *Magellania fragilis*, *M. joubini*, and *Liothyrella uva* from 200 m depth, all had very low mean percent cover, between 2.2% and 3.3%. There was, however, a striking difference between the valve epibiota of *M. fragilis* and *M. joubini*. This was the difference in taxonomic community structure. The community structure of epibiota (in terms of proportion of each major taxon) on *N. lecointei* is very similar to that on *M. joubini*. These two brachiopods are dissimilar in all major respects, which suggests their community structure is 'typical' of hard substratum epibiota in the Weddell Sea and highlights the peculiarity of the community on *M. fragilis*. The high interspecific but low intraspecific variation of epibiotic cover and community structure on living brachiopods in one broad site may provide an insight into the structure of deep-sea epibiotic communities. These results may also be of considerable help to palaeontologists in interpreting the degree of *pre* and *post mortem* epibiotic colonization of valves.

The encrusting epibiota on the two New Zealand species, *Notosaria nigricans* and *Neothyris lenticularis*, differed considerably in prevalence, percent cover and community structure. However, epibiotic cover between the Antarctic deep-sea terebratulids and the New Zealand *N. lenticularis* was remarkably similar. This suggests epibiotic communities of similar substrata in different deep-sea locations may vary much less than equivalent shallow-water communities from different localities, and that the epibiota of the rhynconellid *N. nigricans* is different from the terebratulids, and also local habitat hard substrata.

(*d*) *Attachment substratum*

Lee (1990) described macro- and microsubstratum as the most important influences on New Zealand brachiopod distribution and survival respectively. Erect bryozoans were considerably the most important attachment substrata for the Antarctic articulate species studied here. This may be because erect bryozoans are highly abundant in many Antarctic shelf locations (Bullivant 1961, 1968; Winston & Heimberg 1988). It is of particular note that conspecific attachment, in contrast to shallow-water populations, was rare and that brachiopods were occasionally attached to sponges and even echinoid spines. The majority of specimens of the two New Zealand study species were not attached to any substratum, possibly because they are recorded as degenerating their attachment to become free-living (Dell 1951; Neall 1970). An unattached habit, either partly embedded in sediment or lying free on the sea-floor would have a profound influence on epibiota. It is also possible, however, that many specimens may have been dislodged from rocks during collection, as rocks have been identified as a generally preferred substratum (Lee 1990). Although little can be definitely said of the substrata for the New Zealand species, the Antarctic specimens indicate that erect bryozoans provide an important deep-water substratum for brachiopod populations, which in turn act as an important substratum for encrusting bryozoan, polychaete and foraminiferan populations.

(*e*) *Conclusions*

The prevalence and percent cover of epibiota decreased with depth. The taxonomic structure of epibiotic communities also changed with depth. The colonization of most articulates was very low compared to brachiopods previously studied from shallow water. Similarities in levels of colonization and epibiotic community structure between deep-sea species from Antarctica and New Zealand, suggest a cosmopolitan nature to epibiota of deep-sea brachiopods. There is evidence that valve architecture and ornamentation significantly increases cover by epibiota and that punctae have negligible influence. Bryozoans, foraminiferans and polychaetes were the most abundant colonizers and rigid erect bryozoans were used as an important source of attachment substrata.

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