RESEARCH PAPER

Latitudinal and depth gradients in marine predation pressure

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ABSTRACT

Aim There is a general paradigm that marine predation pressure increases towards the tropics and decreases with depth. However, data demonstrating global trends are generally lacking. Rhynchonelliform brachiopods inhabit all the oceans and often survive shell-crushing predator attacks. We investigate shell repair in brachiopods across a range of Southern Hemisphere and tropical Northern Hemisphere latitudes and depths.

Location The Southern Hemisphere and tropical Northern Hemisphere.

Methods We analysed the frequency of shell repair in 112 bulk samples, over 70% of which showed traces of shell damage and repair.

Results The pattern of shell repair frequency (RF) was more complicated than the anticipated increase with decreasing latitude, with low levels at both polar and tropical sites but high levels at temperate latitudes. This pattern is only evident, however, in shallow water assemblages; and there is no latitudinal trend in water depths greater than 200 m, where shell RF is systematically low. There was a significant logarithmic relationship between RF and depth. Low polar repair rates reflect reduced predation pressure, directly supporting the global paradigm. Low rates in the tropics appears counter to the paradigm. However, tropical brachiopods are generally very small (micromorphic) in shallow water and below the minimum size at which damage is recorded anywhere.

Main conclusions Predation pressure decreased logarithmically with depth. At shallow depths (< 200 m) RF showed its highest levels in the mid temperate latitudes with decreasing frequency towards both the tropics and the poles. Low levels of shell repair at high latitudes are likely to be due to a lack of crushing predators, but in the tropics it is suggested that the low frequency is a result of the small size of tropical brachiopods. We hypothesize that micromorphy in this region may be an outcome of high predation pressure.

Keywords
Durophagous predation, latitudinal gradient, rhynchonelliform brachiopods, shell damage, shell repair, tropical, polar.

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INTRODUCTION

Predation is a major factor in all ecosystems on Earth and predation pressure has been identified as a major structuring influence on marine benthic communities over both evolu-

tionary and Recent time-scales (Vermeij, 1987; Stanley, 2008). Seminal work by Paine (1966) and MacArthur (1972) focused on perceived general latitudinal gradients in predation pressure in modern benthic marine environments, whilst other studies

focused on specific groups of predators, notably fish (Bakus, 1969; Palmer, 1979) and gastropods (Bertness *et al.*, 1981; Kelley & Hansen, 2007), or particular groups of prey, notably molluscs (Vermeij, 1987; Alexander & Dietl, 2001a).

Aronson *et al.* (2007) used a lack of key predators (i.e. decapods and crushing fish) to infer reduced predation pressures in the Antarctic and explain the dominance of 'primitive' suspension feeding communities; other studies have shown high levels of predation at tropical latitudes (Peterson *et al.*, 2001; Sanford *et al.*, 2003). Building on these observations, Freestone *et al.* (2011) excluded predators from experimental sites. They demonstrated that intense predation pressure in the tropics reduces species richness on the seabed by a factor of at least two, whereas there was no difference in species richness in the presence or absence of predators at temperate latitudes. These types of exclusion experiments require large amounts of time and resources, especially for sufficient replication to be achieved to allow quantification of variation at sites or in regions. Despite significant efforts at various sites to produce quantitative estimates of predation pressure, studies demonstrating global patterns are lacking (Schemske *et al.* 2009; Freestone *et al.*, 2011).

There is also a general consensus that the diversity of predators (and therefore predation pressure) on benthic prey is greater in shallow waters (Vermeij, 1987; Aronson & Blake, 2001). Again data to support this assertion are relatively sparse, although a few studies do exist (Kropp, 1992; Oji, 1996). There are considerable difficulties in collecting data on predation in deep water and most conclusions have been drawn from the composition of fauna collected in dredges and the necessarily limited observations made from deep submersible or remotely operated vehicle dives. Data focusing on particular kinds of predatory activity and those which seek to use consistent methodologies over large depth ranges or spatial areas are mostly lacking.

One alternative way of gaining further insight into patterns of predation pressure across global regions and from different depths is to assess damage and repair resulting from failed attacks (Vermeij *et al.* 1980; Alexander & Dietl, 2001b, 2003; Stafford *et al.*, 2015). This is a potentially powerful source of data, and has been used by palaeontologists (e.g. Vermeij *et al.*, 1980; Alexander, 1981; Harper, 2005), but there are few studies exploring latitudinal patterns in predation pressure in modern settings, despite them being hindered less by time and spatial averaging than their palaeontological counterparts.

In this study we examined bulk samples of rhynchelliform brachiopods from a wide range of localities and depths throughout the Southern Hemisphere and from low Northern Hemisphere latitudes. Rhynchonelliform brachiopods are an ideal group for this type of investigation. They are present in all the world's oceans and range from intertidal to abyssal depths. Despite often being thought to be undesirable prey (e.g. McClintock *et al.*, 1993; Peck, 1993), they are attacked by a range of durophagous (shell crushing) predators (see Harper, 2011; Tyler *et al.*, 2013) and distinctive scars on their shells record their ability to survive and repair some attacks

(Harper *et al.*, 2009). Our aims here were to examine patterns of repair as a proxy for predation pressure, both within and between species at a range of geographical scales (single locality to cross hemisphere) and depths, and to use these data to test the following hypotheses: (1) predation pressure, as evidenced by repair frequency (RF), decreases with increasing latitude; (2) predation pressure, as evidenced by RF, decreases with increasing water depth.

We also used our data to examine variation in RF within a species across a range of geographical scales and also between species at particular localities. Previous studies on variation in RF have concentrated on gastropods and bivalve molluscs and have identified considerable variation over a range of spatial scales (Schmidt, 1989; Cadée *et al.*, 1997) and between co-occurring taxa with different morphological characters (Vermeij, 1982a; Alexander & Dietl, 2001b). These studies have been aimed on fairly small-scale areas to assess the relative impacts of predation on co-existing species. Our primary aim here has been to address global patterns.

MATERIALS AND METHODS

The frequency of repair of rhynchonelliforms was assessed for 112 samples of single species from sites across the Southern Hemisphere and low-latitude Northern Hemisphere sites (Fig. 1). Detailed sample localities, depths and current storage locations are given in Appendix S1. All but one were bulk samples collected for other purposes. Although we did not undertake an exhaustive taxonomic survey and revision of species names, our data set comprises approximately 55 species, with the majority (87%) being terebratulides.

For each sample, all intact bivalved individuals were carefully examined, with a binocular microscope where necessary, for evidence of repaired shell damage using the rationale discussed by Harper *et al.* (2009). Disarticulated valves and individuals showing unrepaired breakage were discounted (< 1% of individuals in all samples) from the survey because of uncertainty about whether the damage was caused at the time of collection. Repairs were recognized where there had been definite damage to the margins of the shell (or much more rarely punctures through the valve) which had been repaired by subsequent shell deposition. Such breakages are often accompanied by a major disturbance growth line. We avoided counting specimens which had gross valve distortion but no loss of shell material because these were probably caused by overcrowding or deformation associated with parasites. This approach to the recognition of repaired damage is conservative and may slightly underestimate RFs, in particular of very small areas of damage.

For each individual showing repaired damage we recorded the number of repairs and categorized each as *marginal* (i.e. originally sustained at the valve edges) or *punch-holes* (i.e. sustained at some point distant from the valve edges). If two (or more) damage events were initiated at the same growth line but on different points around the valve margins, these were counted together as a single injury event.
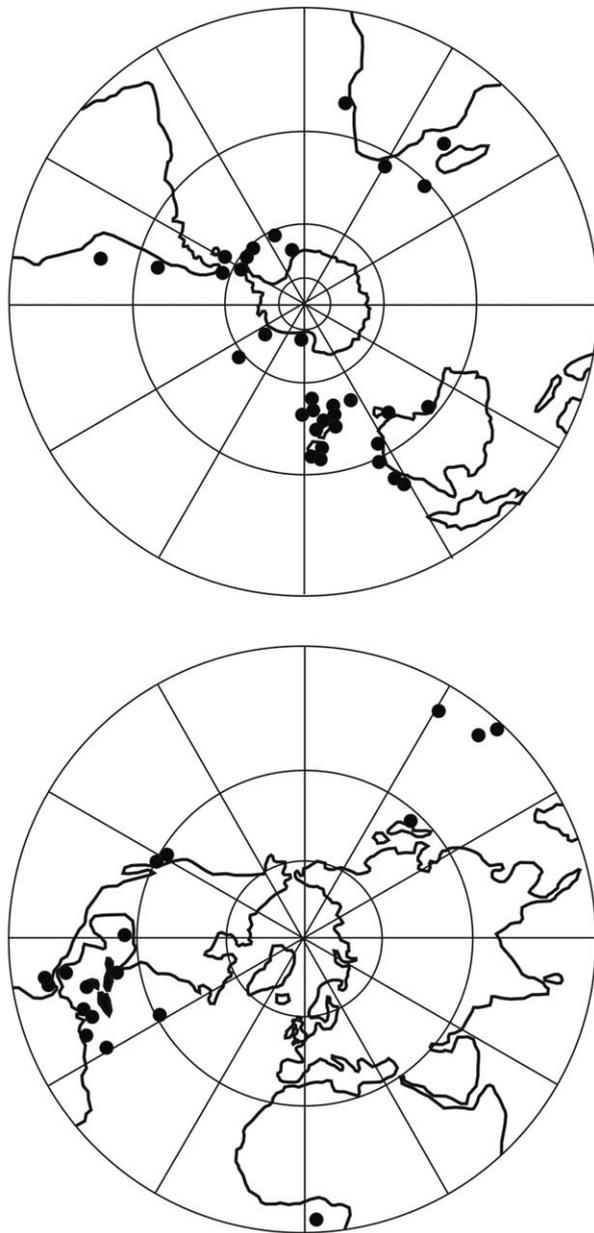
Figure 1 Locations of sampling sites. Because of the close proximity of some samples not all sampling points are visible. Full details of latitude and longitude, water depth and taxon for each are given in Supporting Information.

For each sample we calculated RFs using the two metrics currently in widespread use, namely the proportion of individuals (N_d) in any sample bearing one or more repaired injuries and the total number of injuries sustained within a sample divided by the number of individuals in the sample (N_i). The relative merits of these two metrics are difficult to assess, so both were calculated in order to provide comparable data for future studies, as recommended by Alexander & Dietl (2003).

Data were analysed in three depth bins: 0–199 m, 200–999 m and ≥ 1000 m with the aim of exploring the continental shelf, slope and deep water habitats. Where samples were collected by

Figure 2 Individual of *Magellania venosa* from Chilean fjords (ventral valve length 38 mm) showing cleft style repaired margin damage.

dredge over a specified depth range we used the minimum depth recorded.

RESULTS

We examined 12 955 individual brachiopods comprising 112 different samples of single species. All RF data (N_i and N_d) and the occurrence of drill holes are given in Appendix S1. Of these samples, 79 (i.e. 70.5%) contained individuals with repaired valve damage. The proportion of damage repair recorded at any one site varied between samples from 0 (in 33 samples) to 0.687. Virtually all repairs involved damage caused to both valves simultaneously and were located at the valve margins, typically as either clefts or scallops as defined by Alexander (1981) (Fig. 2). In our analyses we use N_i as the measure of RF, but because most of our samples were dominated by individuals showing only one repair per individual the results are essentially the same when assessed using N_d.

Repair frequency with depth and latitude

Our data (Figs 3 & 4) show clear depth and latitude patterns. RF is lower at deeper sites; less than 0.09 in all samples from depths of more than 200 m and less than 0.03 in those beyond 1000 m, and for these two depth classes 45% and 54% of samples, respectively, have no repairs. By comparison, those from a water depth of less than 200 m show a much greater range of RF – from 0 at 16 sites (i.e. 20.3%) to a maximum of 0.687 in a sample of *Terebratella dorsata* from a depth of 18 m from the Falklands Islands. In fact for samples from the shallowest depth bracket (0–199 m), RF values were notably higher in those samples collected at depths of less than 100 m. Plotting all non-zero data on a logarithmic scale shows a highly significant relationship ($P < 0.0001$) between depth and RF (Fig. 3b).

There is no apparent latitudinal pattern in samples from water depths of over 200 m (Fig. 4). Those from less than 200 m (i.e. from the continental shelf), however, show an uneven latitudinal distribution of N_i, with low levels RF that range only as high as 0.1 for both the higher latitudes over
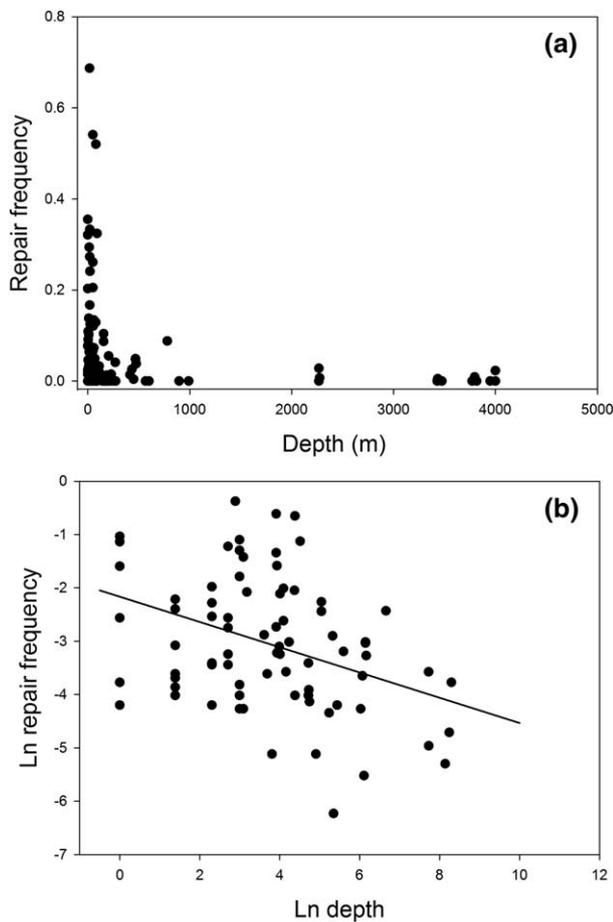
Figure 3 Frequencies of samples of rhynchonelliform brachiopods with repaired damage in relation to water depth ($n = 112$). (a) Raw repair frequency (RF) data (%) plotted versus depth (m). Note that all samples with RF > 0.105 occur in populations living at depths of less than 100 m. (b) Data shown in (a) replotted after ln transformation of both variables (zero values are excluded). A strong linear relationship is evident where ln RF = $-2.167 - 0.237$ ln depth ($r^2 = 14.6$, $F_{1,77} = 13.16$. $P < 0.00001$).

65° and for the tropical latitudes below approximately 20°. For the intervening mid latitudes, some samples also showed low RF but the total range was much higher (Fig. 4).

The variation in RF with latitude seen in shallow water (depths less than 200 m) can be analysed by splitting the data into 10° latitude bins and testing for differences between bins. RF data were not normally distributed because of the presence of zero values. After dividing the data into 10° bins, they were logit transformed in MINITAB and a generalized linear model showed that RF values were significantly different between bins ($F = 3.07$, d.f. 78, $P = 0.007$).

Intraspecific repair frequencies over geographical areas

We examined our data for particular taxa that had been collected from different sites across a range of geographical scales. One sample of 427 individuals of *Liothyrella uva* from Signy
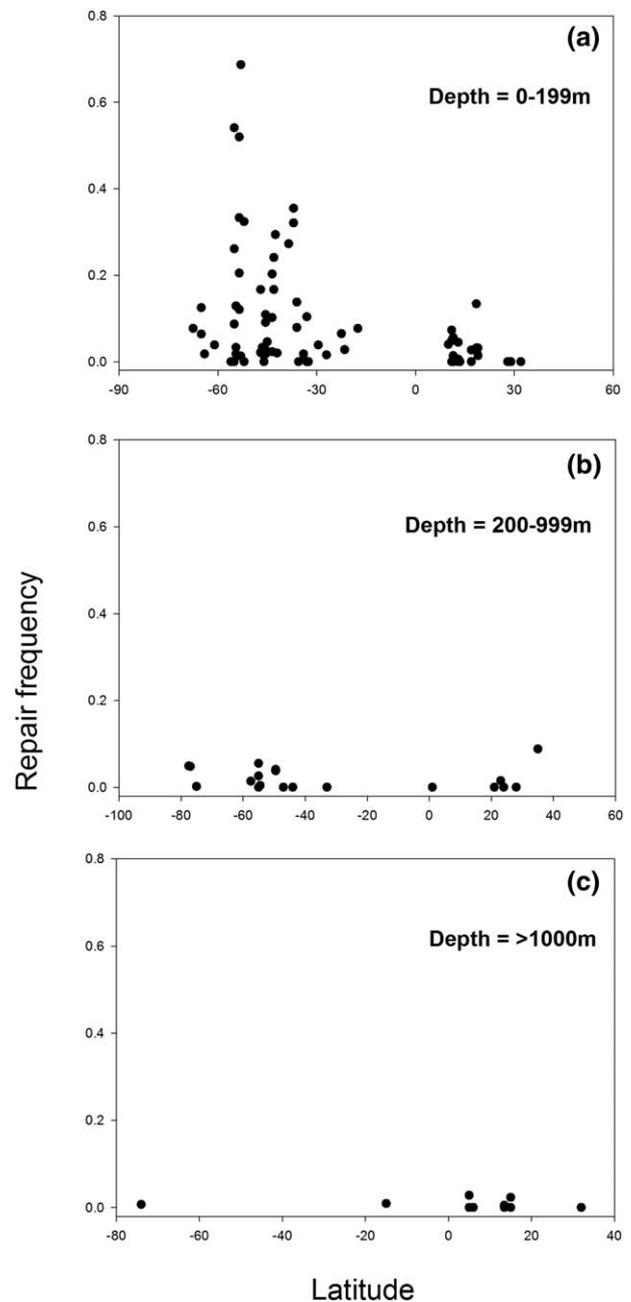

Figure 4 Repair frequency in samples of rhynchonelliform brachiopod species ($n = 112$) plotted against latitude. Data are split into three different depth classes: (a) 0–199 m, (b) 200–999 m, and (c) deeper than 1000 m. Although at depths greater than 200 m there is relatively little variation in repair frequency, in shallow water there is a marked latitudinal pattern where frequencies are low in the tropical and polar regions but markedly variable and higher in the mid latitudes.

Island, in the South Orkneys (60°43′ S, 45°37′ W) (Appendix S1) in fact comprised subsamples collected from seven discrete locations separated by a maximum distance of 2.5 km within Borge Bay and all from depths between 3 m and 25 m. Only nine individuals came from the Lurky Rocks site so these were excluded from further analysis, but the RFs were calculated for

each of the remaining six localities, showing a range from 0 to 0.081 (mean = 0.046; SE = 0.013; data in Appendix S2).

Other taxa were also sampled multiple times within their distributional range. Amongst these were seven taxa for which at least five samples were analysed (Appendix S3) and which encompassed a very large proportion of the distributional range of the taxon. For each of these, although there was variation in the RFs recorded, the standard errors were all small.

Different taxa in same sampling locality

Another question that is commonly posed in the literature which we were able to address with our data was whether the RF differs between coexisting species at a particular sampling site. *Magellania venosa* and *Terebratella dorsata* occurred together in mixed clumps in sites south of the Falkland Islands as they do elsewhere in their range (Försterra *et al.*, 2008). Of the two, *M. venosa* had a RF (0.439) almost twice that of *T. dorsata* (0.235). In Doubtful Sound, New Zealand, brachiopods occur in mixed species communities (Lee *et al.*, 2010), including *Liothyrella neozelanica* and *Terebratella sanguinea*. Our data for these two species indicate RFs of 0.148 for *T. sanguinea* and 0.076 for *L. neozelanica*, again with one species having a RF nearly twice that of the other.

DISCUSSION

Shell damage and repair were evident in over 70% of the 112 samples of rhynchonelliform brachiopods that we examined from a wide range of latitudes and depths. There is a logarithmic relationship between RF and water depth. Repair was most frequent in samples from continental shelf depths, and in these samples there is a marked latitudinal variation, with low levels of damage and repair at polar and tropical latitudes and high levels only recorded in the mid-latitudes.

The interpretation of shell repair and its significance is not always straightforward (Alexander, 1981; Vermeij, 1982a; Alexander & Dietl, 2001b). In particular it may be difficult to determine the exact cause of the shell damage, especially to discriminate between that caused by failed durophagous predation and that by abiotic agents in the environment, such as saltating clasts (Harper *et al.*, 2009). While this may be problematic for single cases it often is possible with careful inspection of patterns and styles of damage (Alexander & Dietl, 2003). For most of the samples in this study repair is infrequent, but for those samples where the number of repairs is sufficient (the Antarctic Peninsula and Falkland Islands) we have been able to analyse the patterns involved and suggest that the style and size distribution at the time of repair suggests that failed crushing predation is the likely cause (Harper *et al.*, 2009). Although it is possible that some of the intertidal and very shallow subtidal samples might have been damaged by waves moving large clasts or, in polar regions, ice, it is unlikely that this is responsible for the majority of damage seen here where the main type of damage was to both valves being marginally 'nipped' rather than

showing the type of blunt force trauma, randomly located on the shell, reported for bivalves suffering impacts from the physical environment (Harper *et al.*, 2012). The majority of the repaired damage surveyed in our study is thus most likely to have resulted from failed predation.

There is a further paradox associated with the interpretation of shell repair noted by Alexander (1981). Samples showing zero or low rates of repair might indicate populations that experience very low levels of predation, or, alternatively, that the predators involved are extremely efficient and that attack failure is rare. This paradox is difficult to resolve, particularly without field surveys at specific sites. However, studies of crushing predators reviewed by Vermeij (1982a,b) reveal that in natural habitats across the latitudinal range crushing fish and crustaceans fail frequently and Stafford *et al.* (2015) demonstrated a good correlation between repair and predation in gastropod molluscs. Our previous work (Harper *et al.*, 2009) has demonstrated that the predators involved show good evidence of size selectivity and that at some sites multiple repairs are not infrequent. These factors suggest that survival rate is high for brachiopods (indeed rather better than for bivalve molluscs) and that RF is a good metric for quantifying predator activity in rhynchonelliforms.

Rhynchonelliform brachiopods have traditionally been viewed as suffering very little mortality due to predation. They have a very low flesh yield, in particular compared with other similar prey items such as bivalve molluscs, and their tissues often contain high levels of carbonate spicules (Peck, 1993). There is also evidence that their flesh may contain chemicals that deter predator attack (McClintock *et al.*, 1993). Nevertheless there is good evidence in the literature that extant rhynchonelliforms are eaten by a variety of predators (reviewed in Harper 2011; Tyler *et al.*, 2013). In our survey only 23% of samples showed neither shell repair nor predatory drill holes (see below). Mortality rates have been demonstrated to be low (less than 1% a year) in mark–recapture experiments (Peck *et al.*, 1997), but these studies have been restricted to polar seas where our data indicate, and previous studies have inferred, that predation pressure is low (Aronson & Blake, 2001). Size distributions of populations of rhynchonelliforms are often left skewed, suggesting low levels of mortality at larger size classes and the possibility of a size refuge from predation (Harper *et al.*, 2009). Although rhynchonelliform brachiopods may be less favoured prey it is clear that they are attacked by a range of predatory taxa and importantly, in the context of this study, across a range of latitudes (Harper, 2011).

Published data, from both single gastropod species sampled over a range of geographical distances (from vicinal to several hundred kilometres apart) and from different species at the same site, indicate that there is clear variation in levels of repair at the same site and over spatial scales (Vermeij *et al.*, 1980; Vermeij, 1982a; Schmidt, 1989; Cadée *et al.*, 1997). This is likely to reflect variations of habitat, predator and prey densities, predator attack preferences and specific prey defences, as well as the localization of other prey taxa that predators may attack in preference. This emphasizes the need for caution in

amalgamating these types of data from localities and regions. An argument that these data are robust, however, comes from our data for single brachiopod species that cover a wide range of their distributional ranges and show relatively small standard errors. Further to these data, different RFs for co-occurring taxa from the Falkland Islands demonstrated large differences in the RF recorded, with the value for the smaller but thicker-shelled *T. dorsata* being half that for the larger, smooth thin-shelled *M. venosa*. Harper *et al.* (2009) suggest that for both taxa there is good evidence to indicate that the damage is caused by failed predation. It is not clear whether the difference in frequency is related to any preference in attack, either for species or size of prey, different 'success' rates for multiple predators or differences in the reparability of different prey species, but all these factors may affect the results. Data for the co-occurring taxa *T. sanguinea* and *L. neozelanica* from fjords in New Zealand also showed very different frequencies of repaired damage. However, in this instance the more robust *T. sanguinea* had almost twice as high a frequency of repair as *L. neozelanica*. This suggests that if the factors here governing attack are similar to those in the Falkland Islands then shell thickness is not a major factor in dictating the level of attack in these species.

Variation across latitudes

Latitudinal gradients are an important and widely recognized theme in both terrestrial and marine ecosystems, with strong evidence for higher diversities and increased interaction between organisms in low tropical latitudes compared with high-latitude polar regions (e.g. Dobzhansky, 1950; Pianka, 1966; Hillebrand, 2004; Schemske *et al.*, 2009). This has led to a general paradigm which suggests that predation pressure decreases with latitude (Vermeij, 1987; Freestone & Osman, 2010). However, despite this being one of the most widely quoted paradigms in this field, studies demonstrating the reduction in predation pressure across latitudes from tropics to poles are generally lacking (Schemske *et al.*, 2009; Freestone *et al.*, 2011). The expected trend was reported by Vermeij *et al.* (1980) who demonstrated that RFs in terebrid gastropods are greatest in tropical settings. Visaggi & Kelley (2015) also found an equatorward increase in predatory drill holes made by naticid gastropods in bivalve prey along the Brazilian coast. Kelley & Hansen (2007), on the other hand, showed a peak of drill holes in bivalve prey in the Carolinian province in a latitudinal survey along the east coast of the United States. Our data show a more complex pattern, with a clear decline in the frequency of repaired attacks from temperate latitudes to both tropical and polar regions (Fig. 4). Although at all latitudes studied there were samples that had no evidence of repaired attacks, only the temperate latitudes (between 35° S and 60° S) had samples with RFs over 15% (Fig. 4). The reduction in RF at high latitude here is consistent with the hypothesis of reduced levels of durophagous predation in the polar regions. A major environmental characteristic structuring marine benthic communities in polar latitudes is significant disturbance in shallow depths from ice (Peck *et al.*, 1999), and it is possible that rhynchonelliforms experience damage from ice impacts in Antarctica. However, the damage seen here is unlikely to be due to that cause, for two reasons. Firstly the type of damage sustained is not consistent with ice impacts which are unlikely to produce damage only at the edges of shells or as matched pairs of damage on each valve, which are the only types of damage identified in this study. In an investigation into iceberg damage to shells of the infaunal Antarctic bivalve *Laternula elliptica* damage was more stochastic in the position of shell breakage and more variable in its extent (Harper *et al.*, 2012). Secondly, polar rhynchonelliforms usually live in habitats that are protected from ice impacts, either in deeper water or in crevices, overhangs and caves (Peck *et al.*, 1997).

The low frequencies of repair at tropical latitudes are not consistent with predictions of an increase in durophagous predation with decreasing latitudes. There are two possible interpretations of the dual observations of a low incidence of repaired damage in low-latitude rhynchonelliforms and the fact that tropical brachiopods (of all three extant clades) tend to be small (i.e. micromorphic); Peck & Harper (2010) reported that that taxa from Southern Hemisphere latitudes of 17° or less contain no species more than 10 mm long. One possibility is that the small size of tropical brachiopods and their cryptic life habit, often in crevices or on the undersides of corals (Zuschin & Mayrhofer, 2009), makes them inaccessible to crushing predators. A second possibility, however, is that micromorphy can be seen as an adaptive response to more generally increasing durophagy at lower latitudes. Harper *et al.* (2009) examined patterns of repaired predator damage in four species of temperate rhynchonelliforms and showed that large size acted as a refuge from predation. However, of the 1290 specimens they examined, only one less than 5 mm long exhibited damage and only seven less than 10 mm long. They also showed that damage occurred at a 'preferred' prey size, which was at a shell length of between 20 and 40 mm depending on prey species, and the incidence of damage was normally distributed about that size, as predicted by optimal foraging theory (Stephens & Krebs, 1986). Crushing and drilling predators that take rhynchonelliforms either as direct prey or because of a mistaken predation attack are, therefore, unlikely to affect specimens less than 10 mm long. These data do not allow us to differentiate between the hypotheses that tropical predators have removed large rhynchonelliform brachiopods or that small size is an adaptation to high levels of predation pressure. What they do strongly infer is that the lack of rhynchonelliforms in tropical latitudes is due, one way or another, to high levels of durophagous predation pressure, supporting the general paradigm.

Variation with depth

Our data very strongly support the hypothesis that predation pressure is greatest at shallower water depths (Vermeij, 1987; Oji, 1996), as RFs in rhynchonelliform populations at

the shallowest depths studied here are nearly an order of magnitude higher than at the deepest depths (Fig. 3) and the pattern of a high range of RF on the continental shelf mid-latitude samples is not apparent in those from deeper water. Other studies have also suggested that crushing predation reduces with depth (e.g. Kropp, 1992) and deep waters are often proposed to be key refuges (Vermeij, 1987; Aronson & Blake, 2001), although higher RFs have been recorded in molluscs from deep sea vent sites (Rhoads et al., 1982) and Vale & Rex (1988, 1989) report high RFs in gastropods on the upper continental slope. As far as we are aware, our data allow the first calculation of a relationship between an index of predation pressure (RF in rhynchonelliform brachiopods) and depth. The best fit to our data is a power relationship between increasing water depth and decreased predation pressure with a slope of -0.237 (i.e. $RF = 0.114D^{-0.237}$, where RF is expressed as a percentage and D is the depth in metres), indicating that predation pressure changes very rapidly with depth in shallow environments but very little with depth in continental slope or deep sea habitats.

Although Peck & Harper (2010) identify a reduction in brachiopod size with increased water depth this change is not as pronounced as that seen latitudinally within the shallow water brachiopods at low latitude, and the size of individuals in deep water is still well above that where significant repairs are seen in shallower depths. The size reduction also becomes apparent at rather greater depths than the fall off in RF seen in this study. In this case there is no reason to suggest that the diminutive size of many deep water taxa is due to predation pressure.

Although the primary focus of this paper was shell repair, because data on predation on brachiopods are so seldom published (Harper, 2011) we also took the opportunity to record the incidence of predatory drill holes in our samples (Appendix S1). These data are unsuitable for further analyses because the samples were collected live. This means that they record largely only incomplete drill holes and, contrary to repaired damage frequency, failure of drilling predation once commenced, and when a discernible drill hole is apparent, is relatively uncommon on brachiopods (Harper, 2005; Harper et al., 2011). As such recording the frequency of incomplete drill holes is likely to be a poor proxy for predation pressure. Nevertheless, it is interesting to note that 31 samples contained evidence of drilling predation. Drilled samples were from either the continental shelf or the upper parts of the slope, with only four of them (i.e. 12.9%) from depths greater than 200 m and, of those, only one from more than 250 m, at 450 m. Drilled samples occurred across the latitudinal range from 13° to 75°. Thus these data broadly echo the more exhaustive RF data detailed here.

CONCLUSIONS

Our data from the frequencies of repaired damage in rhynchonelliform brachiopods show that over 70% of brachiopod

bulk samples exhibit evidence of repair following crushing predatory attack. Predation pressure decreased markedly with depth, and there is a strong logarithmic relationship between RF and depth. The pattern of shell repair at shallow depths (< 200 m) shows high levels in mid temperate latitudes with decreasing frequency towards both the tropics and the poles. Low levels of shell repair in polar latitudes is a result of there being few crushing predators, but in the tropics probably reflects the small size of rhynchonelliform species living there. We hypothesize that micromorphy of brachiopods in the tropics is a likely outcome of intense durophagous predation pressure in this region.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Raw data used in analyses.

Appendix S2 Detailed breakdown of repair frequency from individual sampling sites in the Signy Island bulk sample.

Appendix S3 Mean repair frequency and latitudinal range of samples for species for which there are data across a broad geographical range.

BIOSKETCH

Liz Harper and **Lloyd Peck** have complementary interests in exploring the distribution and relationships been organisms over both Recent and geological time-scales. Liz primarily uses bivalves and brachiopods in studies of predator–prey relationships and biomineralization. Lloyd studies the evolution, adaptation and genomics of the unique biodiversity of the polar regions. He has 17 season's experience in Antarctica and two in the Arctic.

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