

## PATTERNS OF UNREPAIRED SHELL DAMAGE IN RECENT BRACHIOPODS FROM FIORDLAND (NEW ZEALAND)

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*Abstract.* In order to provide quantitative data concerning patterns of shell breakage and repair in rhynchonelliform brachiopods, we studied undisturbed death assemblages from a New Zealand fiord complex where three species of terebratulide and one rhynchonellide occur in dense mixed patches on the near vertical walls. Proportions of damaged (both repaired and non-repaired) individuals varied between both taxa and sampling site. However, the general observation was that few individuals show signs of having been able to repair damage but the proportion of individuals showing unrepaired, and hence presumably fatal, breakages was higher (up to 76% in *Magasella sanguinea* from one sample from Tricky Cove in Doubtful Sound). Damage was mostly concentrated around the anterior margins and affected both valves and is consistent with having been clamped between a set of either jaws or claws. Potential culprits include fish (wrasse), rock lobsters and echinoids. As yet it is unclear whether the damage results from deliberate feeding activity or as collateral damage from grazers feeding on other organisms on the fiord walls which may allow secondary predation by asteroids. The net effect is, however, the same, in that the damage appears to have been fatal. More structured sampling is now required to understand the spatial variation in this damage and mortality, and also to establish the culprits with more certainty.

## INTRODUCTION

Biotic interaction is widely thought to be a major selective force in evolutionary processes (e.g., Vermeij 1987; Jablonski 2008; Taylor 2016) with Stanley (2008) arguing that predation is more important than competition. Although evidence for predation is well known in Palaeozoic brachiopods (e.g., Brunton 1966; Alexander 1981, 1986a,b; Baumiller et al. 1999) far less is known about predation in post-Palaeozoic brachiopods. This is unfortunate because of the long-standing suggestion that the failure of rhynchonelliform brachiopods to flourish towards the present day is due to the increased predation pressure of the Mesozoic Marine Revolution

(Stanley 1974, 1977; Vermeij 1978; Donovan & Gale 1990; Lee 2008; Vörös 2010). This later suggestion has, however, been countered by arguments that brachiopods are unattractive prey, particularly compared with the bivalve molluscs (Thayer 1985; Peck 1993), and so predation pressure is likely to have been too weak to have had a direct impact on the clade (James et al. 1992; Kowalewski et al. 2005).

One of the limitations for testing such ideas has been a general lack of data on predation on brachiopods from both modern and post-Palaeozoic samples. In the last 20 years however, there has been a more concerted effort to collect data and this has shown that at least some brachiopod communities are targeted by predators (Harper & Wharton 2000; Baumiller & Bitner 2004; Harper 2005; Baumiller et al. 2006; Tuura et al. 2008; Harper et al. 2009; Harp-

er & Peck 2016; Gordillo et al. 2019). Nevertheless, observations and data are frequently scattered in the literature, often in contributions where the primary focus is elsewhere (e.g., Bitner 2007, 2008, 2009).

The majority of previous studies of predation on post-Palaeozoic brachiopods have focussed on the activities of drilling predators because their activities can be relatively easily traced in both death and fossil assemblages because of their readily recognised drill holes (Harper 2016). There have been far fewer studies of the effects of shell crushing predation on post-Palaeozoic brachiopods despite direct observations of crushing predators, such as crustaceans and fish, attacking modern brachiopods (Simões et al. 2001; Coelho Rodrigues & Simões 2010) and observations of brachiopod debris in gut contents of fish and crustaceans (Daniels 1982; Witman & Cooper 1983; Arnaud & Miquel 1985; Davis & Wing 2012). Additionally, Paine (1969, p. 339) concluded from the pattern of shell damage that the majority of individuals in a population of *Terebratalia transversa* off Seattle had been attacked by crabs. However, attempts to collect predator-prey interaction data of successful crushing predation (of brachiopods or indeed of any other prey taxa) have generally proved challenging because of the difficulty of recognising fatally damaged shells, in particular distinguishing those damaged by predators and those which have been damaged by post mortem biostratinomic processes. Most studies have, instead, attempted to quantify levels of crushing predation by collecting data on repaired damage resulting from failed predation attempts (Alexander 1981, 1986a, b; Taddei Ruggiero 1990; Kowalewski 2002; Taddei Ruggiero & Bitner 2008; Harper et al. 2009; Harper & Peck 2016). However, two potential problems are inherent in such studies. Firstly, such surveys need to distinguish between failed predation damage and other causes of pre-mortem breakage such as saltating clasts and ice (Raffaelli 1978; Shanks & Wright 1986; Cadée 1999) and, in modern assemblages, also anthropogenic damage, such as by fishing or dredging activity (Ramsay et al. 2001). It is never possible to ascribe a source to every instance of damage, but it is possible, with sufficient data, to establish patterns of breakage which suggest predatory activity (Alexander 1981, 1986a,b; Harper et al. 2009; Harper & Peck 2016). Furthermore, even if it is possible to recognise and quantify the frequency of failed crushing predation in any population or sample, the

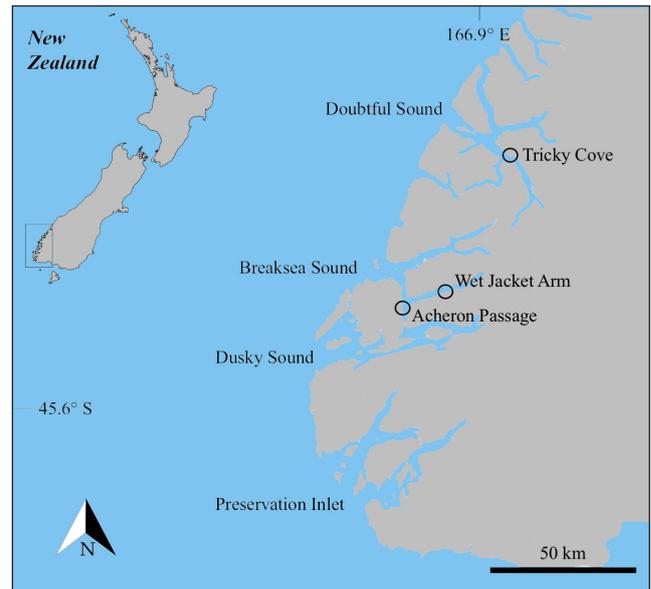


Fig. 1 - Locations of sampling sites within Fiordland, South Island New Zealand.

second problem is the well-known paradox articulated by Alexander (1981) that low repair frequencies might indicate either low attack rates or the activities of a very successful predator and so there is no simple, or even generally applicable rule, that repair frequency is a good proxy for the activities of crushing predators.

In this paper we use death assemblages of rhynchonelliform brachiopods collected from the fiords of South Island, New Zealand to study patterns of post-mortem shell damage. These samples are of interest because they come from one of the most extensively studied modern brachiopod faunas (Richardson 1981; Lee et al. 2010; Harper et al. 2011; Baird et al. 2013; Robinson et al. 2016). Specifically, our samples have been collected from ledges on the fiord walls and are likely to have suffered relatively little post-mortem disturbance making it possible to investigate shell damage sustained either at, or just prior to, death. This opportunity is particularly interesting as these fiords host a wide range of potential predators representing a relatively intact predator fauna associated with an extensive marine reserve network in Doubtful Sound (Wing & Jack 2014), thus presumably giving a good indication of natural interactions and processes. Our study aims to collect data on the style and the frequency of unrepaired damage in a range of taxa at different localities within the fiords.

Tab. 1 - Sample details and data for both repair and unrepaired damage. Drill holes are also recorded.

Locality/Taxon	Number of articulated individuals examined	Number of individuals showing repairs (Repaired Damage Frequency)	Number of individuals showing unrepaired marginal damage (Unrepaired Damage Frequency)
<b>Doubtful Sound</b>			
<b>Espinosa</b> 45°19'19.84"S;167°00'34.71"E Depth: 15-18 m			
Sample 1 (collected: February 2008)			
<i>Magasella sanguinea</i>	85	5 (0.06)	11 (0.13)
<i>Calloria inconspicua</i>	59	4 (0.07)	12 (0.20)
Sample 2 (collected: February 2008)			
<i>Magasella sanguinea</i>	28	Not recorded	3 (0.11)
<i>Calloria inconspicua</i>	37	Not recorded	8 (0.22)
<b>Tricky Cove</b> 45°20'47.84"S;167°02'38.09"E Depth: 18-20m			
Sample 1 (collected: February 2008)			
<i>Magasella sanguinea</i>	39	Not recorded	25 (0.71) 2 drill holes
<i>Calloria inconspicua</i>	32	Not recorded	19 (0.59)
<i>Notosaria nigricans</i>	15	1 (0.07)	4 (0.27)
Sample 2 (collected: February 2008)			
<i>Magasella sanguinea</i>	113	5 (0.04)	63 (0.56)
Sample 3 (collected: April 2008)			
<i>Magasella sanguinea</i>	74	2 (0.03)	38 (0.51) Plus 3 drill holes
<i>Calloria inconspicua</i>	42	0 (0)	20 (0.48) Plus 2 drill holes
Sample 4 (collected: February 2010)			
<i>Calloria inconspicua</i>	57	1 (0.02)	24 (0.42)
<i>Magasella sanguinea</i>	85	5 (0.06)	11 (0.13)
<b>Dusky Sound</b> All collected by CW Thayer in January 1993			
<b>Wet Jacket Arm</b> Depth of 18 m			
<i>Magasella sanguinea</i>	55	13 (0.24)	42 (0.76)
<i>Liothyrella neozelanica</i>	26	1 (0.04)	4 (0.15)
<i>Notosaria nigricans</i>	17	0 (0)	2 (0.12)
<b>Acheron Passage</b> Depth of 18 m			
<i>Notosaria nigricans</i>	30	0 (0)	7 (0.23)
<i>Calloria inconspicua</i>	20	0 (0)	3 (0.15) Plus 2 drill holes

## LOCATION

All samples were collected from the Doubtful Sound/Dusky Sound fiord complex from the western coast of South Island, New Zealand (Fig. 1). Here the vertical rock walls of the fiord support

a dense epifauna (Fig. 2A, B); at shallow depths (less than 3 m) mussels, algae and barnacles dominate but below this there are dense aggregations of brachiopods, ascidians, sponges, bryozoans and corals (Grange et al. 1981; Witman & Grange 1998; Lee et al. 2010). The occurrence of the mussels is strong-

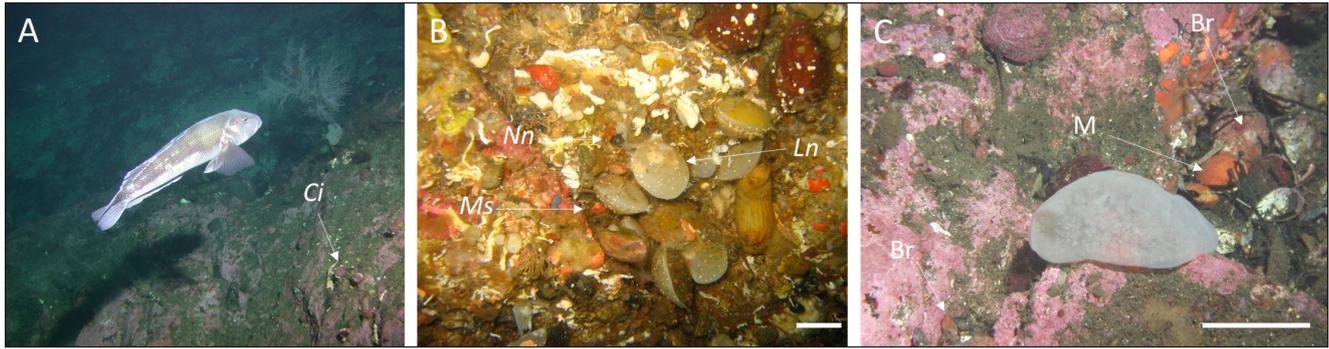


Fig. 2 - A) Typical inner-fiord rockwall community showing *Calloria inconspicua* (Ci) individuals (35 mm) attached in small groups at 15 m. B) Mid-fiord rockwall community showing dense, multi-species brachiopod assemblages at 19 m depth, including *Liothyrella neozelanica* (Ln), *Notosaria nigricans* (Nn) and *Magasella sanguinea* (Ms). C) Collection of shell debris at 20 m depth showing the presence of articulated and disarticulated valves of dead brachiopods (Br) and bivalves (M). Scale bar indicates 50 mm.

ly controlled by the low salinity layer that offers a refuge from the activities of a variety of predators (including diverse fish, starfish and spiny lobsters) which patrol at deeper depths and are excluded from the low salinity layer (Witman & Grange 1998). The epifaunal cover is patchy, perhaps controlled by the frequency of slippage of rock debris during earthquake-induced landslides causing relatively sparse areas (Smith & Witman 1999), whereas more well-established epifaunal patches are found below areas of stable vegetation on the fiord sides (Lee et al. 2010).

In terms of physical disturbance, the narrow confines of the fiords limit wave action and there is little tidal movement, meaning that the shells of animals living on the rock wall detach after death and accumulate on horizontal ledges as death assemblages which lie relatively undisturbed (Fig. 2C). These deposits are dominated by the shells of the mussel *Mytilus galloprovincialis* but also contain those of numerous brachiopods.

## MATERIALS AND METHODS

Samples of shell debris were collected by hand by SCUBA divers from ledges at various sites from Fiordland (see Fig. 1 and Tab. 1). In Doubtful Sound, collections were made, specifically for this project, during fieldwork carried out in February and April 2008 and February 2010 (Fig. 2C and 3). For each sample, non-brachiopod material was discarded and recognisable brachiopod debris sorted by taxon. Similar shell debris material (accumulated brachiopod material but already sorted of other debris) from Dusky Sound sites that had been collected by C.W. Thayer in January 1993 and now in the collections of the Department of Geology, University of Otago, was also investigated. In any sample, brachiopod taxa represented by less than ten individuals were discounted.

For each taxon in each sample, we made counts of the num-

ber of recognisable individuals. In practice an individual was counted if the posterior part of the shell was present and at least part of the two valves remained articulated. Isolated fragments were ignored. Each individual was then scored as either apparently undamaged, damaged by the removal of shell material or damaged and repaired. The last category was recognised using the protocol of Harper et al. (2009) whereby, briefly, repaired damage was distinguished from other shell deformities, such as those caused by over-crowding (Lee 1978) together with clear signs of loss of shell. The style of each damage (repaired or not) was recorded as either being marginal or punctured. From these data we calculated two metrics for each species: Repaired Damage Frequency (number of individuals with repaired damage/total number of individuals) and Unrepaired Damage Frequency (number of articulated individuals with unrepaired breakage/total number of individuals). Frequencies are presented as a proportion, ranging from 0 to 1.00. We also took the opportunity to record the incidence of predatory drill holes in the brachiopod shells.

## RESULTS

We collected data from 8 death assemblages, giving us a total of 17 individual species samples, which includes terebratulides (*Liothyrella neozelanica*, *Calloria inconspicua* and *Magasella sanguinea*) and the rhynchonellide *Notosaria nigricans* (see Tab. 1 and Fig. 1). The most represented taxa were *Magasella sanguinea* and *Calloria inconspicua* (7 species samples each) which probably reflects their abundance and distribution in the Fiordland communities (Lee et al. 2010) but also their robust, relatively thick, shells. Only one sample had sufficient numbers of individuals of *Liothyrella neozelanica* for the study. This may reflect the fact that this species is both less common and more patchy in its distribution (Grange et al. 1981, and M. Lamare, personal observations) but also that this species is relatively thin-shelled and therefore may have a shorter taphonomic half-life than the other taxa.

Fig. 3 - Example of a death assemblage from Espinosa Point (Doubtful Sound) after sorting of brachiopod material (largely of *Magasella sanguinea* and *Calloria inconspicua*).



### Style of shell damage

All species samples contained individuals that showed unrepaired damage (Fig. 4). In almost all cases this was in the form of pieces of shell removed from the anterior margins. In other instances, and sometimes in conjunction with anterior breakage, damage was in the form of punctures away from the valve margins. In all examples, the damage had clean, jagged edges (backed up by preliminary observations with scanning electron microscopy which showed angular breaks to the fibres rather than being 'rounded' and corroded). Areas of damage typically affect both valves (though not necessarily to the same degree) and usually show more shell loss than areas of repaired shell damage (see Fig. 4D).

A number of samples from both Tricky Cove and Acheron Passage also showed evidence of predatory drill holes of the type described and illustrated by Harper et al. (2011, their Figure 2). These neat circular holes ranged between 0.8 and 2.0 mm in diameter and all completely penetrated the shells. The incidence of these drill holes is recorded in Tab. 1.

### Frequency of shell damage

Tab. 1 records the numbers and frequency of unrepaired damage in all samples, and also, where available, for repaired damage.

## DISCUSSION AND CONCLUSIONS

The southwestern fiords of New Zealand represent an example of an intact marine ecosystem,

relatively undisturbed by anthropogenic activity through the establishment of a network of marine reserves within New Zealand's largest national park (Wing & Jack 2014), that has minimised the impacts of fishing and of coastal development. Therefore, the populations we studied have a relatively intact and diverse predator fauna including fish, asteroids, crustaceans and gastropods and thus provide an opportunity to gather data on natural rates of predation on brachiopod communities. Additionally, the relatively low energy fiord environments with minimal wave and current activity allow the accumulation of dead shells on accessible ledges, which are reasonably free of post-mortem or collection damage.

### Source of damage

All species samples showed some degree of unrepaired damage, mostly to the anterior part of the shells of some individuals. The sharp jagged edges are consistent with mechanical trauma. This marginal damage affects both valves (although not necessarily symmetrically) and is evidently highly localised rather than occurring around all the valve margins. These characteristics do not suggest that it results from shell disintegration brought about by fibres being released by the decay of their organic sheaths, as described by Collins (1986) and Emig (1990). Rather they suggest that the valves have been crushed between two opposing hard surfaces, most likely the jaws or claws of a predator. They are similar to damaged Argentinean brachiopods illustrated

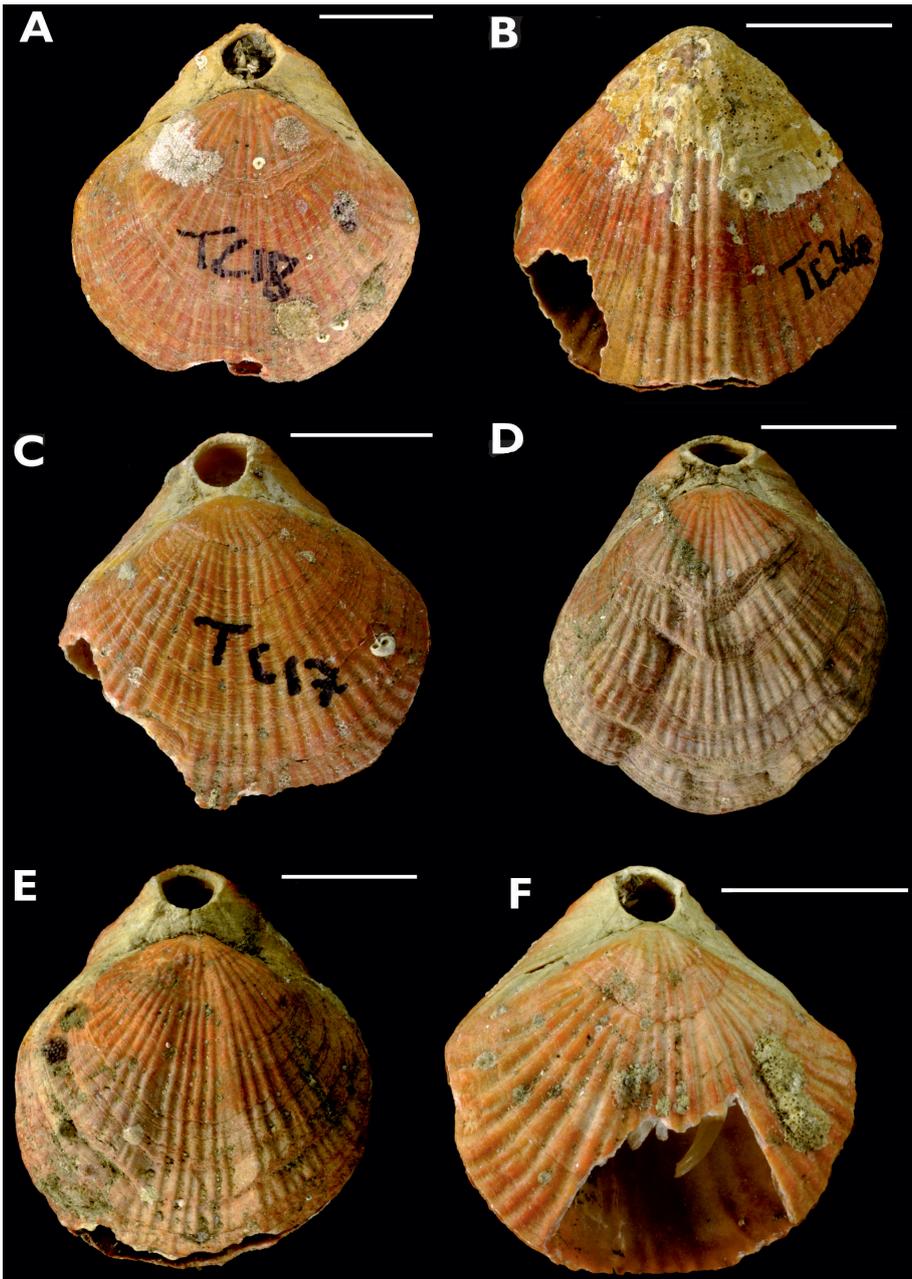


Fig 4 - Examples of damaged *Magasella sanguinea* from Tricky Cove, Doubtful Sound, all collected February 2008, Sample 1. Scale bars indicate 10 mm.

by Gordillo et al. (2019, their Figure 7) which they also interpret as having been caused by shell crushing predators, such as fish, octopods and crustaceans. There is a similar range of possible candidate taxa for the damage we observed but the most likely would seem to be benthic grazing fish. Indeed, Davis & Wing (2012) report debris of *Magasella sanguinea* in the guts of the Scarlet Wrasse *Pseudolabrus miles* which co-occurs in the sampled localities. There are also other potential predators that would come in contact with brachiopod populations in Doubtful Sound, including sea urchins (*Evechinus chloroticus*) and rock lobster (*Jasus edwardsii*), while Witman & Grange (1998) reported that *Evechinus* grazes indis-

criminate on sessile shelled taxa, mainly mussels, leaving jagged breaks and is responsible for significant mortality at 5 m depths in Tricky Cove. Similarly, *Jasus edwardsii* is capable of handling shelled taxa, including live mussels (James & Tong 1998), and was found to graze on shelled taxa (blue mussels) in Tricky Cove, leaving fragmented shell debris.

Tricky Cove also harbours other potential predators including the abundant sea star, *Coscina-sterias muricata* (Witman & Grange 1998) which is certainly capable of feeding on damaged brachiopods in aquaria (Harper 2011). We also recorded drill holes in several of our samples, in particular

in *Magasella sanguinea*. These are typical in scale and morphology of those produced by muricid gastropods, and are the same as those recorded from similar death assemblages from Tricky Cove studied by Harper et al. (2011) which were attributed to the trophonid *Xymene ambiguus*. However, neither the starfish nor gastropod predators are likely to cause the type of shell damage reported in this study and can be discounted as culprits.

Clearly there is scope for further work to try to elucidate the exact culprit(s) responsible for the damage observed.

### Direct or accidental predation?

It has been a popular notion that brachiopods are not favoured prey items (Thayer 1985; Peck 1993) and that any predation that occurs is secondary either as accidental or mistaken events (Kowalewski et al. 2005; Simões et al. 2007). Although several more recent papers have highlighted evidence that several modern groups do appear to actively target brachiopod prey (Harper et al. 2011) the fact remains that, despite the direct evidence of brachiopod debris in the guts of *Pseudolabrus miles*, there is no certainty that these wrasse or the rock lobsters were feeding directly or intentionally on them. A number of other studies citing direct evidence for predation of brachiopods by fish, crabs and sea urchins suggests that they may have been ingested accidentally (e.g., Daniels 1982; Witman & Cooper 1983; Arnaud & Miquel 1985; Fouke & La Barbera 1986). However, the damage we have observed is not the result of accidental ingestion, rather damage made to the valve margins which has frequently not been subsequently repaired. It is therefore possible that it is simply collateral damage that resulted from the fish and sea urchin grazing on the abundant epifauna growing both on and between the brachiopods, which includes encrusting sponges, ascidians, polychaete tube worms and crustose coralline algae, or perhaps by fish or lobsters which have commenced a 'mistaken' attack but not completed it. However, even if this is collateral rather than direct predation, the net effect is the same in that it appears to have been fatal. If damaged, most brachiopods, like bivalves and unlike gastropods, have a poor capacity for sealing off damaged tissue with the result that leaking blood and body fluids attract secondary predators and scavengers (Vermeij 1983). Although brachiopods are clearly able to repair experimental

marginal damage if they are kept in predator-free tanks (Cross et al. 2015, 2016), Harper (2011) reported that damaged individuals of New Zealand brachiopods held in tanks with starfish (*Coscinasterias muricata* and *Patiriella mortensenii*) and the scavenging gastropod *Cominella glandiformis*, were rapidly attacked and consumed by them (Harper 2011, their Figure 1). It is notable in our samples that there are consistently fewer individuals which have repairs than those which have unrepaired damages and also that the former involved loss of only relatively small amounts of shell material, implying that most damage was too significant to allow repair even if the animal survived the initial attack.

### Frequency of damage

Regardless of whether the damage recorded here was direct predation or incidental breakage, the majority appear to have been fatal to the brachiopods. It is, therefore, of interest to consider the frequency. Perhaps unsurprisingly our data show that the proportion of individuals showing damage varies between sampling sites, different sampling dates and between taxa. It is clear that a much more structured sampling effort would be required to elucidate underlying patterns. Nonetheless it is apparent that frequencies were highest for *Magasella sanguinea* and that in general (apart from one sample) were higher in Tricky Cove and Wet Jacket Arm than either Espinosa or Acheron Passage. This may reflect the abundance of benthic predators; indeed, there is a large lobster population at Tricky Cove, although no quantitative comparisons were made among sites and years as part of this study. Rates of unrepaired damage in Argentina reported by Gordillo et al. (2019) are around 20% and thus those found here, for Tricky Cove in particular, are rather higher, suggesting that it is more important here. Our work suggests that there are differences in frequency between the different sampling sites and in general there is a positive relationship between the frequencies of unrepaired damage in *Magasella sanguinea* and *Calloria inconspicua*. More work however is required to understand these differences and to establish whether there is any 'preference' for particular brachiopod prey taxa or whether there is any 'taphonomic' bias in these death assemblages whereby the more robust taxa are the ones more likely to sustain recognisable damage rather than being fragmented in a much more destructive fashion.

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