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Tolerance rather than competition leads to spatial dominance of an Antarctic bryozoan

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ABSTRACT

Understanding the processes that govern species distributions is a fundamental goal of ecology. Species differ in patterns of resource-use due to differences in response to biotic and environmental factors. Some species dominate favourable habitat through competitively superiority, while others have evolved to exploit niches of abiotic stress where competition is low. We observed interspecific differences in the use of horizontal and vertical habitats by Antarctic bryozoa. The most spatially dominant species, *Inversiula nutrix*, mainly occupied horizontal surfaces, while nine other bryozoan species mainly occupied vertical surfaces. We hypothesized that this spatial segregation may be due to either competitive displacement of other species by *I. nutrix*, or tolerance of *I. nutrix* to an environmental stress associated with horizontal orientation. To investigate this we quantified competitive interactions between all species, and conducted a manipulative field experiment to test effects of sedimentation on bryozoan growth. We found that *I. nutrix* was not a superior competitor, but was more tolerant of sedimentation than were other species. Despite mediocre competitive ability, tolerance to a stressor has allowed *I. nutrix* to occupy resources unavailable to the other species, and thereby gain spatial dominance within the community.

1. Introduction

The question of how biotic and abiotic factors shape species distributions is central to ecology. Understanding the physical and biological processes that structure ecosystems is essential to predicting future change, and such knowledge is increasingly pertinent in areas prone to rapid environmental change, such as polar regions (Steig et al., 2009). Sea-ice dynamics are critically important to shallow polar marine ecosystems (Clark et al., 2013) but are changing in response to climate (Stroeve et al., 2007; Mayewski et al., 2009). In addition, polar seas harbour some of the most remote and least studied ecosystems on earth (Barnes and Clarke, 2011), making it difficult to predict future ecological change. More information on basic processes in polar ecosystems is needed to better understand how species distributions are likely to change in the future.

Relationships between species and their environment can be described with the niche concept (Chase and Leibold, 2003). Hutchinson (1957) described a niche as an n-dimensional space of environmental variables and resources in which a species can persist. He defined two types of niche: fundamental and realised. A fundamental niche is the set of conditions in which a species can persist in the absence of competition; essentially the range of its physiological limits. A realised niche is where a species persists after all factors, including biological interactions, have influenced its distribution. The realised niche is usually a subset of the fundamental niche, because portions of the fundamental niche can be uninhabitable as a result of competition, predation, or other biotic interactions. However, a realised niche can sometimes be larger than the fundamental niche if source populations in good habitats seed those in unsuitable habitats (Pulliam, 2000), or if positive interspecific interactions ameliorate environmental stress (Bruno et al., 2003).

One explanation for the maintenance of species diversity is niche partitioning, where species evolve complimentary patterns of resource use that reduce interspecific competition and increase resource exploitation (Chesson, 2000; Finke and Snyder, 2008). The present study arose from the observation that species of Antarctic bryozoans differed in habitat use, thereby displaying apparent niche partitioning. The most spatially dominant species, *Inversiula nutrix*, mainly occupied horizontal (up-facing) surfaces, while nine other bryozoan species almost exclusively occupied vertical surfaces. Two hypotheses to explain this pattern are that (i) horizontal surfaces are high quality habitat from which *I. nutrix* competitively excludes other bryozoa, or (ii) horizontal surfaces are poor habitat, but *I. nutrix* is tolerant of an environmental stress that other bryozoans are not. *I. nutrix* is almost four times more spatially dominant on boulders in the study area as the next most dominant species (Clark et al., in review), meaning that the mechanism driving this pattern is bearing significant ecological consequences.

Bryozoans are a widespread and diverse component of polar benthic communities, and their competitive interactions have been well studied

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(Barnes and Dick, 2000; Barnes and Arnold, 2001; Barnes and Lehane, 2001; Barnes, 2002). Environmental factors that may contribute to patterns in habitat orientation of bryozoans include sedimentation and light (Glasby, 1999). Sedimentation and light are vertically orientated, so have greater impact on horizontal surfaces due to greater angle of incidence. The site where niche partitioning observed is covered by sea-ice and has very low light (<0.1 μ mol photons m^{-2} day^{-1}) for approximately 11–12 months each year (Clark et al., 2013), so we inferred that sedimentation was the most likely environmental factor driving differences in habitat use.

Sedimentation under sea-ice is mainly in the form of suspended material (marine snow, phytoplankton, macroalgal debris) settling out of the mostly still water column, and detrital sea-ice algae and fauna that fall from the underside of sea-ice to the seabed. Sea-ice heavily reduces physical disturbance and flow, and creates a highly depositional environment where sediment can accumulate for months or years without resuspension. Additionally, diatoms grow in mats on the seafloor (McMinn et al., 2004), often smothering benthic organisms. Sedimentation is recognised as a key factor in temperate and tropical benthic ecosystems (Airoldi, 2003), causing mortality of sessile organisms by smothering and/or interfering with feeding apparatus, but has received less attention as a stressor in polar environments. Some authors have suggested that biogenic sedimentation can impact Antarctic benthic communities (Dunbar et al., 1989; Slattery and Bockus, 1997), but to our knowledge there have been no experimental studies of this.

Alternatively, detrital sediments falling vertically through the water column may be an important food source for benthic species in times of low primary productivity. Primary production under sea-ice is limited due to low light, particularly during winter, and most suspended food comes from detrital sea-ice biota or particles advected from ice-free areas (Riddle et al., 2007). Some species may therefore benefit from exposure to biogenic sedimentation, such as holothurians (sea-cucumbers) that extend feeding appendages into the water column to capture falling sediment (*pers. obs.*). Hence, below-ice sedimentation may act as a stressor, food source, or both.

The way in which sedimentation affects bryozoan communities can be determined by experimentally manipulating sedimentation, and observing effects on species' growth. If *I. nutrix* can grow in the presence of sedimentation but other species cannot, this suggests that the current spatial segregation is due to interspecific difference in tolerance to sedimentation. Alternatively, if all species grow well when exposed to sedimentation, this suggests that species other than *I. nutrix* are excluded from horizontal surfaces due to competition.

To evaluate these hypotheses we conducted two surveys and a field experiment around Casey Station, East Antarctica. We (i) quantified species cover with respect to habitat orientation, (ii) examined competitive interactions and quantified the competitive hierarchy amongst species to test whether the most spatially dominant species was competitively superior, and (iii) quantified sedimentation rates and conducted a field experiment to test whether differences in habitat use between orientations could be attributed to effects of sedimentation.

2. Material and methods

2.1. Study area

This study was conducted around Casey Station in the Windmill Islands (66° 17′ S, 110° 32′ E), on the coast of Wilkes Land, East Antarctica (Fig. 1). The habitat orientation survey, sediment trap measurements, and experiment, were conducted at a site named O'Brien Bay 1 (Fig. 1). This is a sheltered embayment covered by fast sea-ice for the majority (>11 months) or all of the year (Clark et al., 2013). Depth ranges from approximately 5 to 10 m, and seabed consists of gradually sloping granitic gneiss bedrock, boulders and a sediment matrix. A

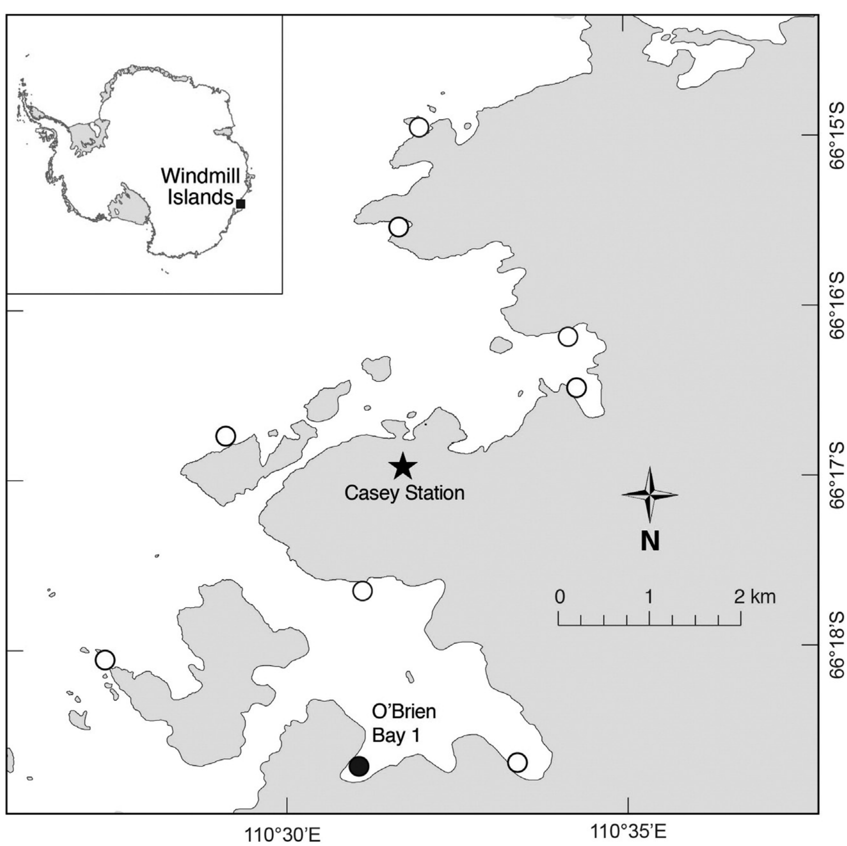

Fig. 1. Map of the study area in the Windmill Islands, East Antarctica. Black circle shows the site of the experiment (O'Brien Bay 1), and competitive interactions were quantified at all sites shown as circles.