

Climate-linked iceberg activity massively reduces spatial competition in Antarctic shallow waters

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Life on Antarctica's coastal seabed rollercoasters between food-rich, open-water, iceberg-scoured summers and food-sparse winters, when the sea surface freezes into 'fast-ice', locking up icebergs, reducing their seabed collisions (scouring). In the last half century, there have been massive losses of winter sea ice along the Antarctic Peninsula, as well as retreat of glaciers and disintegration of ice shelves coincident with rapid recent regional warming [1]. More calving from glaciers and ice shelves coupled with less winter ice should increase scouring of the seabed — which is where most Antarctic species live (<http://www.SCAR-MarBIN.be>). Polar benthos are considered highly sensitive to change, slow growing and all endemic. However, the only published effect of increased scouring on benthos has been increased mortality of the pioneer species *Fenestrulina rugula*, adjacent to Rothera Research station, West Antarctic Peninsula [2] (Supplemental information; Figure S1). It is likely that the recent increase in mortality in this species reflects the mortality of other species on hard substrata. A 2013 survey dive at a nearby locality (Lagoon Island) revealed large areas where no live mega- or macro-fauna could be found, the first time this has been observed there despite being regularly visited by scientific divers since 1997. Here, we report the first assemblage level changes coincident with increased scouring.

On the substrate within the grids of experimental markers, several indicators of assemblage structure were recorded: space occupation by fauna, prevalence and nature of competition and

number of spatial competitors (Supplemental information). These 'indicators' appeared stable up to 2006 but have decreased abruptly since. Mean percentage cover by encrusting fauna was >26% before 2006 and has been <23% since (%cover significantly decreased with increased ice scour; one-way ANOVA, $F = 3.9$, $p = 0.011$). The major space occupiers, bryozoans, dominated this assemblage in terms of richness ($63.2 \pm 0.1\%$ species), space occupied ($71.9 \pm 11\%$ colonised area) and measurable interference competitive encounters (>99%) and thus we focussed on this taxon. About 44% of recruits encountered spatial (interference or contest) competition before 2006 and has declined by 1% per year since (Figure 1; competitive encounters significantly decreased with increased ice scour; one-way ANOVA, $F = 6.6$, $p = 0.001$). However, recent changes go further than prevalence of competitive encounters. The number of species involved in competitive encounters decreased with increased ice scour; one-way ANOVA, $F = 3.6$, $p = 0.016$. The number of competitor identities involved in spatial competition at Rothera has nearly halved from means of $8.75 (\pm 1.53)$ in 1997 to $5.33 (\pm 1.15)$ in 2013. All the species recorded in 1997 were still present in 2013 but many have become so rare that they perform little role in assemblage dynamics, such as spatial competition. Even more fundamental than this, spatial competition has progressively changed from a complex network into a very simple structure over the course of the study period (Supplemental information; Figure S2). Each year more of the pairwise competitive permutations that occurred involved one particular (weak, pioneer) species. The 2013 survey revealed that every interaction involved just one species — amongst the simplest structures of seabed competition reported anywhere. In 2013 more than 96% of the total interactions only involved *F. rugula* (i.e. were intraspecific) and more than 99% of these were intransitive (end in tied rather than decided [win/loss] outcomes; the proportion of interactions being intraspecific significantly increases with ice scour, one-way ANOVA, $F = 41$,

$p < 0.001$). Thus, the outcome of spatial competition has changed from rocks revealing a patchwork quilt of successional stages of overgrowth, and spread by superior competitors, to monopolisation by a single pioneer.

The structure of spatial competition in Antarctic seabed assemblages is unusually hierarchical (i.e. the dominant species overgrew all others, the next overgrew all others apart from the dominant, etc) [3,4]. Also, just one species, a weak pioneer, is involved in 75% of all interactions [4]. The change in assemblage structure reported here means that competition is not really a network anymore. Reduction of complex systems into very simple ones where many (formerly important) species become too rare to maintain meaningful ecological roles is a common reaction to anthropogenic disturbance such as overfishing, pollution, introductions of non-indigenous species and habitat destruction [5]. Across West Antarctica, the levels of these disturbances are among the lowest globally, apart from influences of greenhouse contributions to 'climate change'. There have been predictions of major future responses to climate change by Antarctic benthos, based on sensitivity to experimental manipulated conditions [6], current assemblage composition and recent discoveries of predator densities [7]. However, to our knowledge, this is the first report of hard (time series) data on Antarctic benthic assemblage level changes in response to climate-forced sea ice losses. Where phytoplankton blooms, krill and seabirds occur and how big these areas are is also thought to change in response to regional warming [8]. However, no other climate-forced changes reported from Antarctica have altered the fundamental structure of competition in assemblages. Should the reported major shifts in krill [8] or stone crab [7] abundance and distribution prove to be lasting then they may alter competition in their respective environments — however, preliminary observations suggest the return of strong krill years recently and it is debated whether there is hard evidence of Antarctic

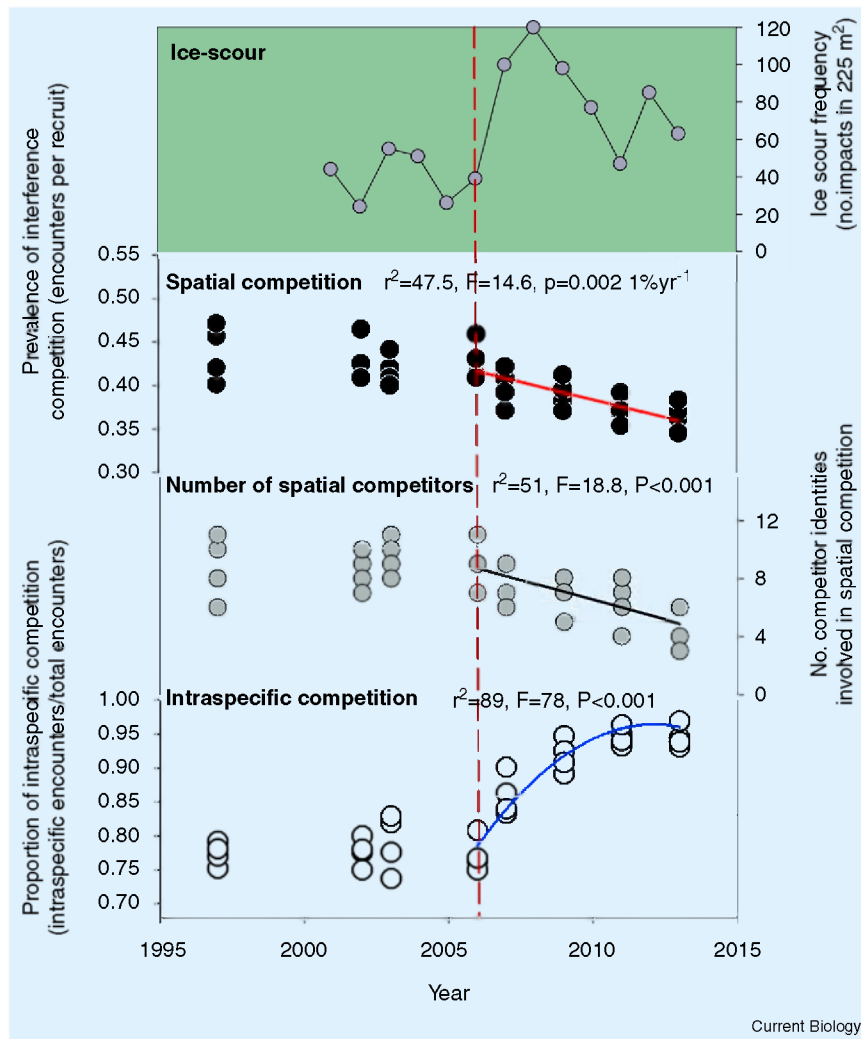


Figure 1. Ice scour and benthic competition with time. Ice-scour frequency, spatial competition, number of spatial competitors and intraspecific competition in shallow water benthos adjacent to Rothera Research station, West Antarctic Peninsula. Relationships are significant regressions (fit of data shown by r^2 values and significance shown by associated ANOVA, F- and p-values).

crabs changing distribution [9]. Most recently, there has been an explosion of colonisation and growth of benthos in areas that formerly underlay ice shelves that have disintegrated [10] — such a major shift in faunal composition would probably also alter the structure of competition.

How scalable are our findings? A new international collaboration between Rothera and Jubany Research Station (South Shetland Islands, Argentina and Germany) should help address this. A replica grid of ice-scour markers, to that at Rothera, has been established near Jubany, where the benthos and fast-ice are monitored.

Antarctic continental shelf habitats are poorly known but rich, and could become a major area of faunistic change if West Antarctic shallows remain among the fastest physically changing areas. Then benthos may have more space due to ice shelf collapses and increased growth from longer phytoplankton blooms. However, warming is likely to also result in species altering their geographic ranges to maintain thermal envelopes. Furthermore, raised atmospheric CO_2 potentially makes secretion of carbonate shells harder (because of acidification). Warming is likely to increase ice scour mortality and reduce assemblage complexity and could aid establishment of non-

indigenous species. We expect the deeper seabed to become richer in benthic colonisation with more iceshelf collapses and fast ice losses, but hard surfaces in the shallows are likely to become deserts dominated by rapidly colonising pioneers and responsive scavengers — with little role for spatial competition or even predation in shaping the structure of such assemblages.

Supplemental Information

Supplemental Information including experimental procedures and two figures can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2014.04.040>.

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