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Disturbance, dispersal and marine assemblage structure: A case study from the nearshore Southern Ocean

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ABSTRACT

Disturbance is a key factor in most natural environments and, globally, disturbance regimes are changing, driven by increased anthropogenic influences, including climate change. There is, however, still a lack of understanding about how disturbance interacts with species dispersal capacity to shape marine assemblage structure. We examined the impact of ice scour disturbance history (2009–2016) on the nearshore seafloor in a highly disturbed region of the Western Antarctic Peninsula by contrasting the response of two groups with different dispersal capacities: one consisting of high-dispersal species (mobile with pelagic larvae) and one of low-dispersal species (sessile with benthic larvae). Piecewise Structural Equation Models were constructed to test multi-factorial predictions of the underlying mechanisms, based on hypothesised responses to disturbance for the two groups. At least two or three disturbance factors, acting at different spatial scales, drove assemblage composition. A comparison between both high- and low-dispersal models demonstrated that these mechanisms are dispersal dependent. Disturbance should not be treated as a single metric, but should incorporate remote and direct disturbance events with consideration of taxa-dispersal and disturbance legacy. These modelling approaches can provide insights into how disturbance shapes assemblages in other disturbance regimes, such as fire-prone forests and trawl fisheries.

1. Introduction

Disturbance events are often conceptualised as departures from a ‘stable’ state, which are discrete and keep the system in flux (White and Pickett, 1985; Newman, 2019). Periodic disturbance is a factor in most natural ecosystems and is a significant selective force influencing assemblage structure and function (Dell et al., 2019). There is an increasing body of evidence that disturbance regimes are changing in frequency, intensity, as well as spatial extent (Webster et al., 2005; Johnstone et al., 2016; Sommerfeld et al., 2018), with further changes predicted into the future (Meehl and Tebaldi, 2004; Moritz et al., 2012; Allen et al., 2015). The majority of disturbance shifts are anthropogenic in origin, caused by factors such as increasing global temperatures, habitat removal, deep-sea mining, fishing pressures and pollution events (Jackson et al., 2001; Buma, 2015; Newman, 2019). To be able to predict the impact of changing disturbance regimes, it is increasingly important to understand the mechanisms underlying disturbance ecology (Turner, 2010; Newman, 2019). This is particularly true in the polar nearshore environment, as ice scour disturbance is predicted to increase

drastically, due to more frequent ice-shelf collapses, fast-ice reduction and glacial retreat (Smale and Barnes, 2008; Barnes, 2017a). In this study we aim to investigate how different components of the disturbance regime influence assemblage structure and how these are intrinsically linked with dispersal capacity of taxa.

Disturbance is probably a key factor in all ecosystems and covers a diverse range of events (Fraterrigo and Rusak, 2008). These are often termed *disturbance regimes* referring to the spatial and temporal variability of disturbance events (Turner, 2010). The intensity, severity and frequency of disturbance regimes have been the focus of numerous studies investigating drivers of community structure (Connell, 1978). Such work has included successional recovery from local disturbances (Sousa, 1984) through to spatial heterogeneity in landscape ecology (Turner, 2005). Insights into disturbance ecology have led to a greater appreciation of how variation in disturbance can lead to major shifts in disturbance-driven spatial and temporal changes in ecological systems (Turner, 2010). However the dynamics of recovery after disturbance events and the importance of local vs remote processes have not been explicitly addressed in the field, although they have been highlighted by

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recent conceptual models (Zelnik et al., 2018). After a disturbance event, recovery is predicted to be dependent on the temporal and spatial scale of the disturbance event (Zelnik et al., 2018). Disturbance events tend to be, in most cases, strongly heterogeneous (e.g. frequency of occurrence) and can occur across vast scales; hence disturbance within the local area may not match that in the wider area. These variations in disturbance levels would change the availability of recruits and adults able to influence recovery, the mechanisms of which, whether by recruitment or re-invasion, are dependent on dispersal capacity of species (Zelnik et al., 2019).

Despite tremendous progress in the research into disturbance, there is still a lack of consensus and understanding, especially when disturbance moves outside of the range of historical disturbance regimes (Bowler et al., 2019). Models have emphasized the importance of mobility and growth of potential colonists, showing that intense frequent disturbance favours mobile species and rapid colonisation (Dayton, 1971; Gutt and Starbans, 2001; Thrush and Dayton, 2002), although these often treat disturbance as a single metric or event (Hughes et al., 2007). By interrogating a single component of disturbance (such as time-since-last-disturbance) and ignoring the influence of adjacent (surrounding) and past disturbance events (Di Stefano et al., 2013), previous studies have failed to more fully capture biodiversity-disturbance interactions. A few studies, particularly in the terrestrial environment, have investigated the importance of surrounding patches by designing ‘refuges’ into their disturbance studies (Sensenig et al., 2017) or have acknowledged that a spatial mosaic will exist within each disturbance regime (Cannon et al., 2017). In this study we investigate a single disturbance regime within the marine system and have incorporated the use of multiple disturbance factors to capture elements of its spatial and temporal variability.

The shallow nearshore waters (<25 m depth) around Antarctica are some of the most naturally disturbed environments on the planet, due to the frequent impacts of icebergs on the benthos, termed “ice scour” (Smale, 2008a). Ice scour has been described as the key controlling factor for benthic communities shallower than 25 m depth (Barnes, 1995; Barnes et al., 1996; Gutt, 2001; Smale et al., 2006; Barnes and Conlan, 2007; Convey et al., 2014; Barnes and Tarling, 2017). These disturbance events tend to be distinct in both time and space, and are highly destructive, with mortality ranging from 60 to 100% (Peck et al., 1999; Lee et al., 2001; Smale, 2008b; Barnes, 2017a). In the shallows, ice scours tend to impact on a small spatial scale formed by small icebergs (termed growlers) but can still be a highly destructive disturbance event. Furthermore the long individual lifetime, relatively low dispersal and high rate of disturbance found in Antarctic fauna creates a natural mesocosm to study the influence of ice scour events in surrounding areas (Potthoff et al., 2006). However climate change is likely to drive the Western Antarctic Peninsula, in particular, through a drastic shift in ice scour, with the retreat of glaciers past their grounding lines (Cook et al., 2005; Barnes et al., 2018).

The interplay between dispersal, disturbance and assemblage structure, have been partly described using conceptual models (Zelnik et al. 2018, 2019) and previous work in terrestrial forests have highlighted their importance (Catano et al., 2017). In the current study we address the Hypotheses: (H1) that the use of multiple disturbance factors can significantly improve the description of resulting assemblage structure. (H2) Dispersal capacity of species alters the relative influence of these disturbance factors on assemblage structure. Using piecewise Structural Equation Modelling we aim to reveal both the direct and indirect effects of disturbance on assemblage structure, to determine whether a multiple factor approach improves our understanding of disturbance and the degree to which it is dispersal dependent.

To capture the spatial and temporal variability within the disturbance regime and isolate local and remote recovery processes, this study divided disturbance regime into three disturbance factors, based on the disturbance of a measured area of sea floor and the sea floor around it: (A) **Recovery Age** the time since the last disturbance event on each area

of sea floor (temporal variability). (B) **Local Disturbance** the proportion of recent disturbance events in close proximity to each area of sea floor. (C) **Background Disturbance** the general level of disturbance that occurs across the wider area. These were chosen as they capture the largest range in spatial and temporal scales available within our data, which are relevant to the differences in dispersal capacity of different groups within the Southern Ocean (more details in appendix S1).

Within this environment we have selected two groups, from the epibenthic assemblage, that both persist under the same disturbance regime but whose individual species have broadly different dispersal capacities. These contrasting dispersal capacities allow the importance of dispersal for recovery to be tested in relation to the disturbance factors A-C. Antarctic benthos typically have relatively low rates of biological and ecological processes, including mobility, when compared with equivalents at lower latitudes, (Arntz et al., 1994; Clarke, 1996). As such a natural mesocosm experiment could be conducted over a relatively small area. The high-dispersal group is a multi-phylum group with mobile adults and pelagic broadcast larvae, potentially uncoupling larval supply from local reproduction (Kuklinski et al., 2014). These larvae have long development times and coupled with a fluid environment, a relatively high dispersal when compared to their low-dispersal counterparts (Stanwell-Smith et al., 1999; Cowen and Sponaugle, 2009; Zhang et al., 2015). The low-dispersal group is a single-taxa group (bryozoa) of sessile adults, all suspension feeders, with cyphonautes larvae which are retained within the benthic boundary layer and therefore have limited dispersal capacity (Kuklinski et al., 2017). Investigation into the recruitment of Antarctic encrusting organisms by Kuklinski et al. (2014) and Kuklinski et al. (2017) demonstrated that bryozoan recruitment occurs in close proximity to adult populations (within meters) due to settling within hours, if not minutes of release (Goldson et al., 2001). (see Appendix S2 and S4 for further detail).

2. Methods

2.1. Disturbance data

Ice scour disturbance was collated over 7 years from 9 separate grids (3 at 5 m depth, 3 at 10 m and 3 x at 25 m), each grid consisted of 25 concrete markers (each identifying a 1 m² grid square or patch of sea-floor). Thus each of the nine grids created a 25 m² monitored area of seabed from the IceBerg Impact Study (IBIS) at 5–25 m depth (Brown et al., 2004; Barnes, 2017a) (Fig. 1). Ice scour events impact these concrete markers, and the number that have been impacted are recorded annually, each December, with any damaged or missing blocks being replaced. The IBIS dataset was used to calculate disturbance factors at 3 spatial and temporal scales (Fig. 2): (A) **Recovery Age** was calculated as the last recorded ice scour event in a 1 m² grid square, as a measurement of direct disturbance, with the assumption that each scour completely destroys that grid square. (B) **Local Disturbance**, the proportion of adjacent grid squares (all 8 surrounding grid squares within 1 m) that have been disturbed in the past year, including the sample grid square. As the IBIS grids (Fig. 2) have sample grid squares in the corners, for which the majority of area around them is unrecorded, these corner samples were removed from the analysis. This disturbance factor was used as a measure of the magnitude of recent adjacent disturbance events, relative to the sample. (C) **Background Disturbance** is the average number of disturbed grid squares within the same IBIS grid, that the sample was collected from, over the 7 years; the largest spatial and temporal scale that data from this study could provide. Background Disturbance is not fully independent of (B) Local Disturbance, as it is on a spectrum, and if you were to increase the spatial and temporal scales of Local Disturbance, eventually the measures would be equal. As the aim was to capture the range of disturbance events and the influence between different temporal and spatial scales, the greatest range was chosen. As ice scour disturbance is extremely stochastic, there was no correlation between these factors.

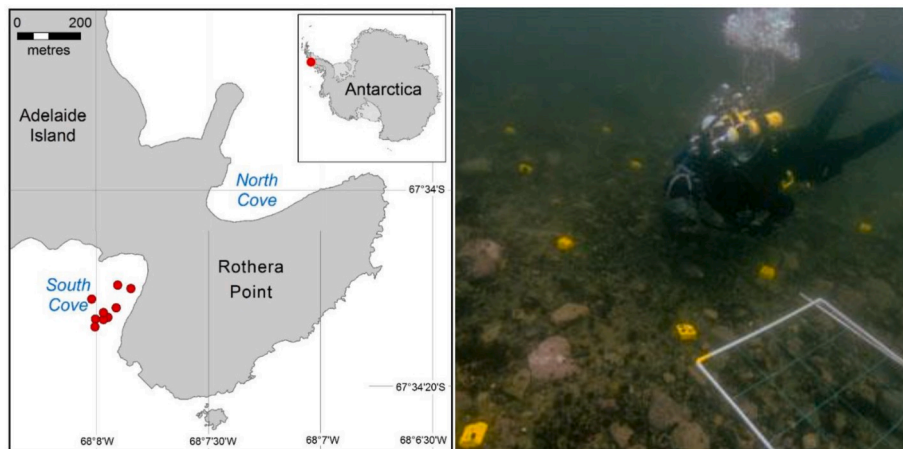


Fig. 1. Map and image of the Iceberg Impact Study grid (IBIS) located within the Western Antarctic Peninsula, Adelaide Island, Ryder Bay.

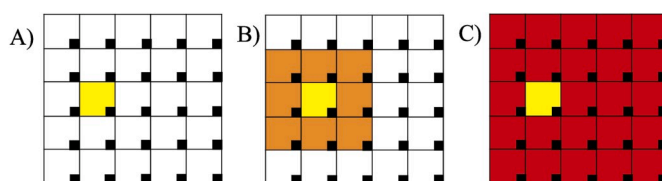


Fig. 2. Conceptual schematic of Iceberg Impact Study (IBIS) grid, with black squares representing the concrete markers. Each concrete marker corresponds to a 1 m² of seabed it represents (not to scale). The yellow square is the example sample grid. Fig. 2A, Recovery Age includes only the sample square itself and records the number of years since it was last hit. Fig. 2B, Local Disturbance includes all adjacent squares (orange), including the sample square (yellow), with the proportion that had been hit in the past year recorded. Fig. 2C, Background Disturbance includes all the squares within the grid (red), including the sample grid square (yellow), and is recorded as the average number of squares that have been hit over the past 7 years. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

2.2. High-dispersal capacity group sampling

Images of the high-dispersal group within each grid square were captured in January 2016 with a GoPro 3+ (GoPro Inc.) in a deepwater housing. Camera lens distortion (fish-eye) was minimised using a calibration lens file and *Hugin* photo editing software. The camera was attached to a modified ROV Deep Trekker Generation 2 Worker (DTG2). Each 1 m² grid square was sampled and scaled using the ROV DTG2 laser scale (av. sample size 0.878 m²). Sample size varied due to differences in the distance between the ROV and seafloor during sampling. Taxa above 5 mm in size (maximum dimension) were identified to species level (2 taxa were unidentifiable to species and kept as morphotypes), from this species richness and densities were calculated.

2.3. Low-dispersal capacity group sampling

The Low-dispersal encrusting group (bryozoans) was sampled from 2009 to 2014. Grid squares were selected to ensure replication across depth, age and disturbance regimes. As bryozoans samples were collected over a 7 year period, the level of disturbance was recorded for each grid from which collections were made, at the time of collection. Due to Background Disturbance being calculated as an average over the 7 years, by definition one value is calculated. After a grid square was selected, SCUBA divers were deployed to retrieve one randomly selected boulder (>10 cm in one axis) from that grid square. Each boulder was examined for encrusting bryozoans, which were identified to species

level (Hayward and Hayward, 1995 and further literature). Bryozoans form multiple colonies, of varying size, on irregular boulder surfaces, so adopting an abundance metric would have introduced a large error. Therefore, a broader presence/absence metric was recorded.

2.4. Selection indicator taxa

The high-dispersal group diversity and abundance was collected across all samples at a single point in time. Whereas the low-dispersal group was a dataset compiled from 7 years of observations with the presence and absence of each species. This allowed the same disturbance histories (Recovery Age, Local Disturbance and Background Disturbance), of both groups, to be calculated for each square. While each group structure was calculated using broadly similar approaches, due to this sampling difference the groups were not directly compared. For each of the groups, indicator taxa were selected, to capture the range of responses across species to each of the disturbance factors. The Antarctic limpet *Nacella concinna* was selected as an indicator taxa as it is the most abundant and conspicuous pioneering species and a key grazer within the shallow benthic community (Suda et al., 2015). *Odontaster validus* was also included as it is the most abundant scavenger/predator (Peck et al., 2008). Both represent two of the largest functional groups within the study environment (Peck et al., 2008) and have well documented larval stages, with *N. concinna* producing planktonic veliger larvae which remain in the water column for at least a month (Suda et al., 2015).

The low-dispersal group is a single-taxa group (Bryozoa) of sessile adults, all suspension feeders, with cyphonautes larvae which are retained within the benthic boundary layer and therefore have limited dispersal capacity (Kuklinski et al., 2017). Investigation into the recruitment of Antarctic encrusting organisms by Kuklinski et al. (2014) and Kuklinski et al. (2017) demonstrated that bryozoan recruitment occurs in close proximity to adult populations (within meters) due to settling within hours, if not minutes of release (Goldson et al., 2001). (see Appendix S2 and S4 for further detail). Three bryozoan species were selected as representative, based on their competitive ability: *Ellisina antarctica* is considered an early pioneer and a poor competitor (Ashton et al., 2017); *Micropora brevisima* a late coloniser and a moderate competitor (Stanwell-Smith and Barnes, 1997) and *Arachnopusia inchoata* a late coloniser and good competitor (Barnes et al., 1996; Bowden et al., 2006) (group details in Appendix S3).

2.5. Piecewise structural equation modelling (piecewiseSEM)

Species were separated into two groups that have different life history traits beyond the discussed dispersal capacity (i.e. body form,

trophic role etc.), making a direct comparison inappropriate. A direct comparison would have also been complicated by differing collection methodologies and temporal variability with the sampling method. Our study therefore focused on the hypothesised mechanisms that determine and influence the observed structure regardless of collection method. Previous studies on disturbance ecology (Dayton, 1971; Connell, 1978; Thrush and Dayton, 2002; Zelnik et al., 2019), especially in high disturbance regimes (Lee et al., 2001; Fairman et al., 2016; Johnstone et al., 2016) and ice scour in particular (Smale et al., 2008; Barnes, 2017a) provided theoretical grounds for the construction of these models. Previous work has indicated the importance of resilience of species in high disturbance environments and the role of succession after the disturbance event. However, we have incorporated three levels of disturbance factors to demonstrate that the relative influence of each is not uniform, and local processes are critical to recovery. To test whether a multi-factor disturbance regime was a valid approach, individual disturbance factors models were compared against observed data. No single factor model adequately accounted for the observed group variability (details in appendix S4). Two hypothesised models were constructed predicting that group structure (species richness and selected indicator taxa) were dependent on a proposed network of interactions from 3 disturbance factors (Background Disturbance, Local Disturbance and Recovery Age). Models were assembled following recommendations from Grace (2006) and Grace et al. (2012), to construct causal networks using ecological theory based on the influence of dispersal and disturbance to define paths of interest. PiecewiseSEM are designed to analyse multivariate hypotheses and are more applicable to responses controlled by multiple factors (Bollen, 1989) and allow testing and construction of conceptual models in a single network (Lefcheck, 2016). Furthermore, the proposed piecewiseSEM paths represent causal relationships (Lefcheck, 2016) and account for correlation between the response variables (Byrnes et al., 2011). In our high-dispersal group *Odontaster validus* abundance was found to correlate with both *Nacella concinna* abundance and overall species richness (Byrnes et al., 2011). With the low-dispersal group all species presence/absence metrics correlated with species richness. Further information on model development, construction and any modification are available in the supplementary material in Appendix S4.

2.6. Model testing

Model evaluation was assessed using Shipley's test of d-separation, which resulted in a Fisher's C statistic that is χ^2 distributed and rejected if below the critical *P* value of 0.05 (Shipley, 2009). Models that were significant, and therefore similar to the observed data, were compared using AIC and BIC fit indexes, with an AIC reduction of >2 considered a significant improvement between the models (Shipley, 2013; Lefcheck, 2016). If there was no difference between the fit indices then the parsimonious approach was adopted, and the model selected was the one with the fewest proposed pathways. Ultimately results and interpretation were based on the model judged to be the best representation of the data. Modifications made to the original conceptual models were guided by the results of the previous single-disturbance factor models and theoretical understanding. Models within the same group had nested factors to allow direct comparison between these models, even when disturbance factors were removed from the analysis. As high- and low-dispersal models were derived from different groups, covariant matrixes, and methods, direct comparisons of covariant regression and fit indices were not appropriate. To test our hypothesis, analysis between the dispersal models proposed, focused on the inclusion and exclusion of disturbance factors and their relative influence on group structure.

3. Results

3.1. High-dispersal group SEM

The high-dispersal group were best described by a combination of the two disturbance factors, Background Disturbance and Local Disturbance (Fisher's $C = 11.451$, $d.f. = 12$, $P = 0.491$, $AIC = 31.451$; Fig. 3. An increase in Background Disturbance reduced the species richness and increased the abundance of the pioneering grazer (gastropod *N. concinna* density). An increase in Local Disturbance correlated with a decrease in the abundance of all species, including the scavenger/predator (echinoid *O. validus*).

3.2. Low-dispersal group SEM

The low-dispersal group required all three disturbance factors to accurately describe the species diversity and indicator taxa observed (Fisher's $C = 22.123$, $d.f. = 16$, $P = 0.139$; Fig. 4). Recovery Age had a strong positive correlation with species richness and all indicator taxa. An increase in Local Disturbance was correlated with decreased species richness and the presence of the pioneering species (bryozoan *Ellisina antarctica*). Conversely, an increase in Background Disturbance was only negatively correlated with the presence of the late coloniser, *Micropora brevissima* (bryozoan).

4. Discussion

Disturbance is well established to be a key influencer of group composition, species richness and other species diversity metrics across realms (land-sea) and latitude (tropics-poles) (Newman, 2019). In an era of increasing disturbance, understanding how an assemblage recovers and persists in the face of natural and anthropogenic disturbance is fundamental for ecology, conservation and ecosystem services (Wang and Loreau, 2016). Yet identifying the underlying mechanisms to explain the relationship between the magnitude of disturbance and specific measures of biodiversity has proved elusive (Yuan et al., 2016). Disturbance regimes are predicted to continue to change and disturbance is expected to increase into the future (Meehl and Tebaldi, 2004; Moritz et al., 2012; Allen et al., 2015). Thus, it is increasingly important to understand the underlying mechanisms linking disturbance, species richness and other drivers of assemblage structure.

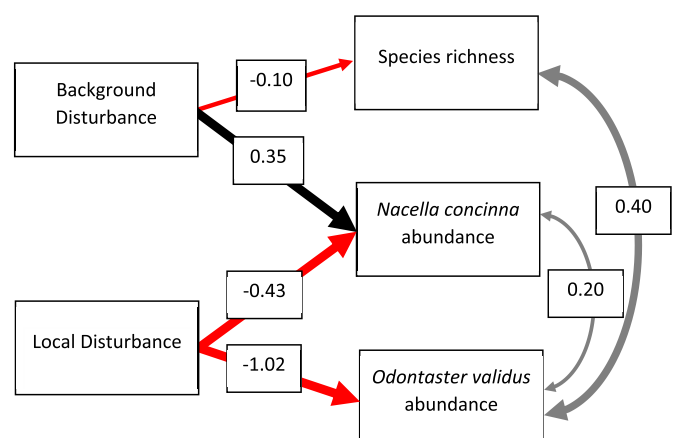


Fig. 3. Path diagram of high-dispersal group model showing how disturbance factors and assemblage structure are associated for the high-dispersal assemblage. Results are from a piecewiseSEM that reproduces the observed variance matrix. Path widths are proportional to regression coefficient shown on the paths. Red representing a negative relationship and black a positive relationship. Double-headed grey arrows represent correlation between two dependent variables, not a casual pathway. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

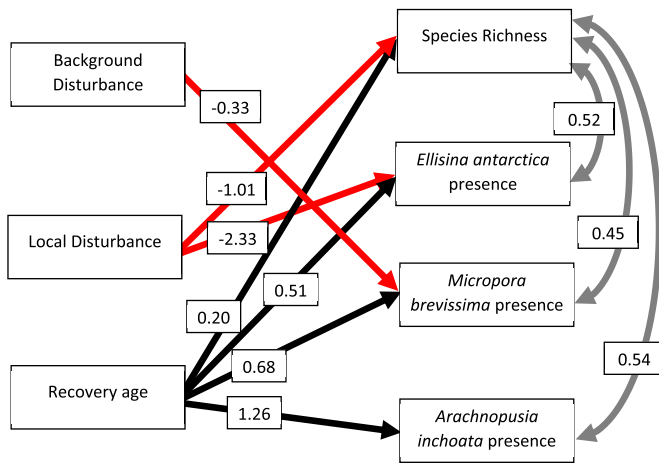


Fig. 4. Path diagram of low-dispersal group model showing how disturbance factors and assemblage structure are associated. Results are from a piecewiseSEM that reproduces the observed variance matrix. Path widths are proportional to the regression coefficient shown on the paths. Red representing a negative relationship and black a positive relationship. Double-headed grey arrows represent correlation between two dependent variables, not a causal pathway. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Our approach revealed that at least two or three disturbance factors acting at different spatial scales drive assemblage composition in our study site, leading to agreement with Hypothesis 1 (H1). Previous studies have suggested that the inclusion of multiple metrics are necessary to fully capture a disturbance regime (Kasel et al., 2017), but this has not been explicitly tested. However, when considering one aspect of the measured high-dispersal group, species richness, a single metric, 'Background Disturbance', was sufficient to describe its variability. As Background Disturbance increases, mobile adults buffer the impact of disturbance across the entire area (Zelnik et al., 2019); re-invading recently disturbed niches. This allows species such as *N. concinna* (gastropod), an r-strategist and pioneering species (Suda et al., 2015) to spread and exploit the resulting lack of competition after the disturbance event. However the capacity for high-dispersal species to recruit or reinvade into these niches could be suppressed if levels of Background Disturbance increase beyond those recorded here, as all but the most resilient, or rapidly recolonising of pioneering species, would be removed (Mackey and Currie, 2001; Hughes et al., 2007).

In such circumstances we expect that biodiversity indices, such as Shannon-Wiener or Simpson's Diversity measures, would correlate well with species richness, as a decreased species richness allows the increasing dominance of a few pioneering species. However, our data also revealed that such a correlation could be misleading, as recent disturbance events adjacent to the study grids (Local Disturbance), although having no influence on species richness, strongly influenced the abundance of the two dominant pioneering species. This explains why diversity-disturbance models can provide different predictions depending on the diversity metrics used (Svensson et al., 2012), as different components of the disturbance regime are addressed.

Recent conceptual models have proposed three recovery paths, that are dependent on the dispersal capacity of the surrounding community (Zelnik et al., 2019), suggesting that the influence of direct or surrounding disturbance events are dispersal dependent. One feature of the low-dispersal group (cheilostomatid bryozoans) is a reliance on benthic larvae (Hayward and Hayward, 1995) to recruit back into recently disturbed areas, and thus their ability to recolonise is spatially limited and dependent on local sources of larval supply. Species richness for the low-dispersal group was influenced by direct disturbance events (Recovery Age), as ice scours would remove the majority of species, followed by secondary succession (Pearson and Rosenberg, 1978).

However, as Recovery Age increases, the formation of a climax community, should ultimately result in a decrease in species richness due to competitive exclusion (Pearson and Rosenberg, 1978). This was not observed, as species richness is only influenced by complete extirpation of a species which does not occur, even under the levels of disturbance measured here; as evidenced by the pioneering species *Fenestrula rugula* (bryozoan) (Barnes and Clarke, 1998) still being present in >90% of samples. In the rare situations of complete shelter from ice scour in shallow waters such pioneers can be completely overgrown by dominant competitors (Barnes, 1995). Recovery of the low-dispersal group is reliant on recruitment by larvae, hence the influence of adjacent disturbance events (Local Disturbance), within close proximity, i.e. within the dispersal range. The current recovery state of adjacent assemblages strongly influences which species are available to recruit into newly scoured sites, hence a decrease in Local Disturbance can allow a greater diversity of species to recruit. By comparing the results of the disturbance models for the two groups (Figs. 2 and 3) it appears that the influence of disturbance factors is indeed dependent on the dispersal capacity of the group. The presence of low-dispersal bryozoan, *Micropora brevisissima*, (late coloniser/moderate competitor bryozoan (Stanwell-Smith and Barnes, 1997)), was, however, influenced by increased Background Disturbance; this is likely due to the rarity of *M. brevisissima* settling on un-colonised (virgin) rock (Barnes et al., 1996). Increased frequency in disturbance events across the wider area and subsequently an increase in the frequency of un-colonised rock would inhibit the ability of *M. brevisissima* recruitment, reducing its presence across the entire area.

Comparison of high- and low-dispersal models (Figs. 2 and 3) reveals that the impact of disturbance on group structure is controlled by different mechanisms, leading to acceptance of Hypothesis 2 (H2). The high-dispersal group is reliant on the spatial spread of mobile adults for recovery, diluting the disturbance across a wider area and homogenising the region, with recruitment from their high-dispersal larvae eventually replacing the lost individuals, across that entire area. Whereas the low-dispersal group required adjacent adult populations to recruit into recently disturbed sites, with disturbance increasing heterogeneity by creating a mosaic of recovering patches. Both patterns have been described in the literature (Zelnik et al., 2019), however in this study we directly link them to the components of the disturbance regime and test the mechanisms behind them. By adopting this approach, previous work by Vause et al. (2019) on marine polar soft sediment communities can be considered from a new perspective. Vause et al. (2019) reported no response of biodiversity to recent ice scour events in a shallow, soft-sediment assemblage, suggesting that this was due to relatively high dispersal of taxa aided by storms and the wash of passing icebergs (Lee et al., 2001) which allowed assemblage to rapidly recover. Our study suggests that the high-dispersal nature of this group would cause them to homogenise across a wider area and that a measure such as Background Disturbance would therefore be more informative. This new perspective can also be applied to disturbance in environments that have disturbance as primary driver in controlling assemblage structure (Fairman et al., 2016; Pulsford et al., 2016). Our results are consistent with the suggestion of Kasel et al. (2017) that only considering the time-since-fire, in forests, (equivalent to Recovery Age) will not capture the full impact of disturbance and that unexplained variation is likely due to surrounding past disturbance events and dispersal capacity. Similar modelling approaches may be applied to other environments where disturbance is a major structuring force (such as trawling activity, fire-prone forests and deep-sea mining), improving our understanding of the mechanisms underlying the impact of disturbance on assemblage structure.

We acknowledge that this study took place in an unusually highly disturbed environment (Brown et al., 2004; Barnes, 2017b), and that the influences identified are likely to change or weaken when considered across entire disturbance gradients. The groups used in this study are both typical components of nearshore communities and have drastically

different dispersal capacity. Future work investigating disturbance should consider multiple components of the disturbance regime, in relation to the dispersal capacity of different taxa under study. Many studies to date have treated disturbance as a single factor, which in some cases may be accurate. However, we advocate that, when considering multi-year assemblages that have developed under repeated disturbance events, the full disturbance regime must be considered. This will be particularly relevant for the Western Antarctic Peninsula, as glacial retreat due to climate change drastically shifts disturbance regimes in the region.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

CRediT authorship contribution statement

Ben J.O. Robinson: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Writing - original draft, Writing - review & editing, Visualization. **David K.A. Barnes:** Conceptualization, Data curation, Writing - original draft, Writing - review & editing, Supervision. **Simon A. Morley:** Conceptualization, Resources, Writing - original draft, Writing - review & editing, Supervision, Project administration, Funding acquisition.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marenvres.2020.105025>.

References

Allen, C.D., Breshears, D.D., McDowell, N.G., 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere* 6, art129.

Arntz, W., Brey, T., Gallardo, V., 1994. Antarctic zoobenthos. *Oceanogr. Mar. Biol.* 32, 241–304.

Ashton, G.V., Morley, S.A., Barnes, D.K., Clark, M.S., Peck, L.S., 2017. Warming by 1 C drives species and assemblage level responses in Antarctica's marine shallows. *Curr. Biol.* 27, 2698–2705 e2693.

Barnes, D.K.A., 1995. Sublittoral epifaunal communities at Signy Island, Antarctica. II. Below the ice-foot zone. *Mar. Biol.* 121, 565–572.

Barnes, D.K.A., 2017a. Iceberg killing fields limit huge potential for benthic blue carbon in Antarctic shallows. *Global Change Biol.* 23, 2649–2659.

Barnes, D.K.A., 2017b. Polar zoobenthos blue carbon storage increases with sea ice losses, because across-shelf growth gains from longer algal blooms outweigh ice scour mortality in the shallows. *Global Change Biol.* 23, 5083–5091.

Barnes, D.K.A., Clarke, A., 1998. The ecology of an assemblage dominant: the encrusting bryozoan *Fenestrulina rugula*. *Invertebr. Biol.* 331–340.

Barnes, D.K.A., Conlan, K.E., 2007. Disturbance, colonization and development of Antarctic benthic communities. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 362, 11–38.

Barnes, D.K.A., Fleming, A., Sands, C., Quartino, M., Liliana, Deregibus, D., 2018. Icebergs, sea ice, blue carbon and Antarctic climate feedbacks. *Phil. Trans. Math. Phys. Eng. Sci.* 376, 20170176.

Barnes, D.K.A., Rothery, P., Clarke, A., 1996. Colonisation and development in encrusting communities from the Antarctic intertidal and sublittoral. *J. Exp. Mar. Biol. Ecol.* 196, 251–265.

Barnes, D.K.A., Tarling, G.A., 2017. Polar oceans in a changing climate. *Curr. Biol.* 27, R454–R460.

Bollen, K.A., 1989. *Structural Equations with Latent Variables*. Wiley, New York.

Bowden, D.A., Clarke, A., Peck, L.S., Barnes, D.K.A., 2006. Antarctic sessile marine benthos: colonisation and growth on artificial substrata over three years. *Mar. Ecol. Prog. Ser.* 316, 1–16.

Bowler, D., Bjorkmann, A., Dornelas, M., Myers-Smith, I., Navarro, L., Niamir, A., Supp, S., Waldock, C., Vellend, M., Blowes, S., Boehning-Gaese, K., Bruehlheide, H., Elahi, R., Antao, L., Hines, J., Isbell, F., Jones, H., Magurran, A., Cabral, J., Winter, M., Bates, A., 2019. The geography of the Anthropocene differs between the land and the sea. *bioRxiv* 432880.

Brown, K.M., Fraser, K.P., Barnes, D.K.A., Peck, L.S., 2004. Links between the structure of an Antarctic shallow-water community and ice-scour frequency. *Oecologia* 141, 121–129.

Buma, B., 2015. Disturbance interactions: characterization, prediction, and the potential for cascading effects. *Ecosphere* 6.

Byrnes, J.E., Reed, D.C., Cardinale, B.J., Cavanaugh, K.C., Holbrook, S.J., Schmitt, R.J., 2011. Climate-driven increases in storm frequency simplify kelp forest food webs. *Global Change Biol.* 17, 2513–2524.

Cannon, J.B., Peterson, C.J., O'Brien, J.J., Brewer, J.S., 2017. A review and classification of interactions between forest disturbance from wind and fire. *For. Ecol. Manag.* 406, 381–390.

Catano, C.P., Dickson, T.L., Myers, J.A., 2017. Dispersal and neutral sampling mediate contingent effects of disturbance on plant beta-diversity: a meta-analysis. *Ecol. Lett.* 20, 347–356.

Clarke, A., 1996. Marine benthic populations in Antarctica: patterns and processes. *Antarct. Res.* 70, 373–388.

Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. *Science* 199, 1302–1310.

Convey, P., Chown, S.L., Clarke, A., Barnes, D.K., Bokhorst, S., Cummings, V., Ducklow, H.W., Frati, F., Green, T.A., Gordon, S., 2014. The spatial structure of Antarctic biodiversity. *Ecol. Monogr.* 84, 203–244.

Cook, A.J., Fox, A.J., Vaughan, D.G., Ferrigno, J.G., 2005. Retreating glacier fronts on the Antarctic Peninsula over the past half-century. *Science* 308, 541–544.

Cowen, R.K., Sponaugle, S., 2009. Larval dispersal and marine population connectivity. *Ann. Rev. Mar. Sci.* 1, 443–466.

Dayton, P.K., 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecol. Monogr.* 41, 351–389.

Dell, J., Salcido, D., Lumpkin, W., Richards, L.A., Pokswinski, S., Loudermilk, E.L., O'Brien, J., Dyer, L., 2019. Interaction diversity maintains resiliency in a frequently disturbed ecosystem. *Front. Ecol. Evol.* 7, 145.

Di Stefano, J., McCarthy, M.A., York, A., Duff, T.J., Slingo, J., Christie, F., 2013. Defining vegetation age class distributions for multispecies conservation in fire-prone landscapes. *Biol. Conserv.* 166, 111–117.

Fairman, T.A., Nitschke, C.R., Bennett, L.T., 2016. Too much, too soon? A review of the effects of increasing wildfire frequency on tree mortality and regeneration in temperate eucalypt forests. *Int. J. Wildland Fire* 25, 831–848.

Fraterrigo, J.M., Rusak, J.A., 2008. Disturbance-driven changes in the variability of ecological patterns and processes. *Ecol. Lett.* 11, 756–770.

Goldson, A., Hughes, R., Gliddon, C., 2001. Population genetic consequences of larval dispersal mode and hydrography: a case study with bryozoans. *Mar. Biol.* 138, 1037–1042.

Grace, J.B., 2006. *Structural Equation Modeling and Natural Systems*. Cambridge University Press.

Grace, J.B., Schoolmaster Jr., D.R., Guntenspergen, G.R., Little, A.M., Mitchell, B.R., Miller, K.M., Schweiger, E.W., 2012. Guidelines for a graph-theoretic implementation of structural equation modeling. *Ecosphere* 3, 1–44.

Gutt, J., 2001. On the direct impact of ice on marine benthic communities, a review. *Polar Biol.* 24, 553–564.

Gutt, J., Starms, A., 2001. Quantification of iceberg impact and benthic recolonisation patterns in the Weddell Sea (Antarctica). In: *Ecological Studies in the Antarctic Sea Ice Zone*. Springer, pp. 210–214.

Hayward, P.J., Hayward, P.J., 1995. *Antarctic Cheilostomatous Bryozoa*. Oxford University Press on Demand.

Hughes, A.R., Byrnes, J.E., Kimbro, D.L., Stachowicz, J.J., 2007. Reciprocal relationships and potential feedbacks between biodiversity and disturbance. *Ecol. Lett.* 10, 849–864.

Jackson, J.B., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., Cooke, R., Erlanson, J., Estes, J.A., 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293, 629–637.

Johnstone, J.F., Allen, C.D., Franklin, J.F., Frelich, L.E., Harvey, B.J., Higuera, P.E., Mack, M.C., Meentemeyer, R.K., Metz, M.R., Perry, G.L., 2016. Changing disturbance regimes, ecological memory, and forest resilience. *Front. Ecol. Environ.* 14, 369–378.

Kasel, S., Bennett, L.T., Aponte, C., Fedrigo, M., Nitschke, C.R., 2017. Environmental heterogeneity promotes floristic turnover in temperate forests of south-eastern Australia more than dispersal limitation and disturbance. *Landsc. Ecol.* 32, 1613–1629.

Kuklinski, P., Balazy, P., Krzemińska, M., Bielecka, L., 2017. Species pool structure explains patterns of Antarctic rock-encrusting organism recruitment. *Polar Biol.* 40, 2475–2487.

Kuklinski, P., Balazy, P., Nowak, M., Bielecka, L., 2014. Factors controlling initial development of Polar bryozoan assemblages. *Stud. Trent. Sci. Nat.* 94, 145–151.

- Lee, H., Vanhove, S., Peck, L., Vincx, M., 2001. Recolonisation of meiofauna after catastrophic iceberg scouring in shallow Antarctic sediments. *Polar Biol.* 24, 918–925.
- Lefcheck, J.S., 2016. piecewiseSEM: piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods Ecol. Evol.* 7, 573–579.
- Mackey, R.L., Currie, D.J., 2001. The Diversity-Disturbance Relationship: is it generally strong and peaked? *Ecology* 82, 3479–3492.
- Meehl, G.A., Tebaldi, C., 2004. More intense, more frequent, and longer lasting heat waves in the 21st century. *Science* 305, 994–997.
- Moritz, M.A., Parisien, M.-A., Batllori, E., Krawchuk, M.A., Van Dorn, J., Ganz, D.J., Hayhoe, K., 2012. Climate change and disruptions to global fire activity. *Ecosphere* 3, art49.
- Newman, E.A., 2019. Disturbance ecology in the anthropocene. *Front. Ecol. Evol.* 7.
- Pearson, T., Rosenberg, R., 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanogr. Mar. Biol. Annu. Rev.* 16, 229–311.
- Peck, L.S., Brockington, S., Vanhove, S., Beghyn, M., 1999. Community recovery following catastrophic iceberg impacts in a soft-sediment shallow-water site at Signy Island, Antarctica. *Mar. Ecol. Prog. Ser.* 186, 1–8.
- Peck, L.S., Webb, K.E., Miller, A., Clark, M.S., Hill, T., 2008. Temperature limits to activity, feeding and metabolism in the Antarctic starfish *Odontaster validus*. *Mar. Ecol. Prog. Ser.* 358, 181–189.
- Potthoff, M., Johst, K., Gutt, J., 2006. How to survive as a pioneer species in the Antarctic benthos: minimum dispersal distance as a function of lifetime and disturbance. *Polar Biol.* 29, 543–551.
- Pulsford, S.A., Lindenmayer, D.B., Driscoll, D.A., 2016. A succession of theories: purging redundancy from disturbance theory. *Biol. Rev.* 91, 148–167.
- Sensenig, R.L., Kimuyu, D.K., Ruiz Guajardo, J.C., Veblen, K.E., Riginos, C., Young, T.P., 2017. Fire disturbance disrupts an acacia ant-plant mutualism in favor of a subordinate ant species. *Ecology* 98, 1455–1464.
- Shipley, B., 2009. Confirmatory path analysis in a generalized multilevel context. *Ecology* 90, 363–368.
- Shipley, B., 2013. The AIC model selection method applied to path analytic models compared using ad-separation test. *Ecology* 94, 560–564.
- Smale, D., 2008a. Spatial variability in the distribution of dominant shallow-water benthos at Adelaide Island, Antarctica. *J. Exp. Mar. Biol. Ecol.* 357, 140–148.
- Smale, D.A., 2008b. Ecological traits of benthic assemblages in shallow Antarctic waters: does ice scour disturbance select for small, mobile, secondary consumers with high dispersal potential? *Polar Biol.* 31, 1225–1231.
- Smale, D.A., Barnes, D.K.A., 2008. Likely responses of the Antarctic benthos to climate-related changes in physical disturbance during the 21st century, based primarily on evidence from the West Antarctic Peninsula region. *Ecography* 31, 289–305.
- Smale, D.A., Barnes, D.K.A., Fraser, K.P.P., 2006. The influence of depth, site exposure and season on the intensity of iceberg scouring in nearshore Antarctic waters. *Polar Biol.* 30, 769–779.
- Smale, D.A., Brown, K.M., Barnes, D.K., Fraser, K.P., Clarke, A., 2008. Ice scour disturbance in Antarctic waters. *Science* 321, 371.
- Sommerfeld, A., Senf, C., Buma, B., D'Amato, A.W., Després, T., Díaz-Hormazábal, I., Fraver, S., Frelich, L.E., Gutiérrez, Á.G., Hart, S.J., 2018. Patterns and drivers of recent disturbances across the temperate forest biome. *Nat. Commun.* 9, 4355.
- Sousa, W.P., 1984. The role of disturbance in natural communities. *Annu. Rev. Ecol. Systemat.* 15, 353–391.
- Stanwell-Smith, D., Barnes, D.K.A., 1997. Benthic community development in Antarctica: recruitment and growth on settlement panels at Signy Island. *J. Exp. Mar. Biol. Ecol.* 212, 61–79.
- Stanwell-Smith, D., Peck, L.S., Clarke, A., Murray, A.W., Todd, C.D., 1999. The distribution, abundance and seasonality of pelagic marine invertebrate larvae in the maritime Antarctic. *Phil. Trans. Roy. Soc. Lond. B Biol. Sci.* 354, 471–484.
- Suda, C.N., Vani, G.S., de Oliveira, M.F., Rodrigues, E., Lavrado, H.P., 2015. The biology and ecology of the Antarctic limpet *Nacella concinna*. *Polar Biol.* 38, 1949–1969.
- Svensson, J.R., Lindegarth, M., Jonsson, P.R., Pavia, H., 2012. Disturbance-diversity models: what do they really predict and how are they tested? *Proc. Biol. Sci.* 279, 2163–2170.
- Thrush, S.F., Dayton, P.K., 2002. Disturbance to marine benthic habitats by trawling and dredging: implications for marine biodiversity. *Annu. Rev. Ecol. Systemat.* 33, 449–473.
- Turner, M.G., 2005. Landscape ecology: what is the state of the science? *Annu. Rev. Ecol. Evol. Syst.* 36, 319–344.
- Turner, M.G., 2010. Disturbance and landscape dynamics in a changing world. *Ecology* 91, 2833–2849.
- Vause, B.J., Morley, S.A., Fonseca, V.G., Jazdzewska, A., Ashton, G.V., Barnes, D.K., Giebner, H., Clark, M.S., Peck, L.S., 2019. Spatial and temporal dynamics of Antarctic shallow soft-bottom benthic communities: ecological drivers under climate change. *BMC Ecol.* 19, 27.
- Wang, S., Loreau, M., 2016. Biodiversity and ecosystem stability across scales in metacommunities. *Ecol. Lett.* 19, 510–518.
- Webster, P.J., Holland, G.J., Curry, J.A., Chang, H.-R., 2005. Changes in tropical cyclone number, duration, and intensity in a warming environment. *Science* 309, 1844–1846.
- White, P.S., Pickett, S.T.A., 1985. Natural disturbance and patch dynamics: an introduction. In: Pickett, S.T.A., White, P.S. (Eds.), *The Ecology of Natural Disturbance and Patch Dynamics*. NY: Academic Press, New York, pp. 3–13.
- Yuan, Z., Jiao, F., Li, Y., Kallenbach, R.L., 2016. Anthropogenic disturbances are key to maintaining the biodiversity of grasslands. *Sci. Rep.* 6, 22132.
- Zelnik, Y.R., Arnoldi, J.-F., Loreau, M., 2018. The impact of spatial and temporal dimensions of disturbances on ecosystem stability. *Front. Ecol. Evol.* 6.
- Zelnik, Y.R., Arnoldi, J.F., Loreau, M., 2019. The three regimes of spatial recovery. *Ecology* 100, e02586.
- Zhang, X., Haidvogel, D., Munroe, D., Powell, E.N., Klinck, J., Mann, R., Castruccio, F.S., 2015. Modeling larval connectivity of the Atlantic surfclams within the Middle Atlantic Bight: model development, larval dispersal and metapopulation connectivity. *Estuar. Coast Shelf Sci.* 153, 38–53.