Rocky islands in a sea of mud: Biotic and abiotic factors structuring deep-sea dropstone communities

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Running head: Deep-sea dropstones
ABSTRACT

Stones released by melting icebergs are called dropstones, and they constitute island-like hard-bottom habitats at high latitudes. In 2012, dropstone megafauna at the HAUSGARTEN observatory in the Fram Strait were sampled photographically. Higher richness, diversity, and abundance of fauna occurred on larger stones and on stones near a deep-water rocky reef. These patterns can be explained by the greater surface area of larger stones, the exposure of larger stones to faster current higher in the benthic boundary layer, and larval supply from the rocky reef. Some pairs of morphotypes co-occurred less often than expected by chance, but while similar patterns have been attributed to interspecific competition in the classical island literature, we cannot draw the same conclusion for dropstones. Instead, non-random co-occurrence on dropstones may be explained by larval dispersal. Dropstone fauna had an overdispersed (clumped) distribution, so pairs of morphotypes may co-occur non-randomly (be found together less often than expected by chance) simply because short larval life and limited dispersal ability prevent them from having randomly overlapping distributions. In addition, we found eight morphotype pairs that co-occurred more often than expected by chance because of commensalism. The patterns found in dropstone communities are reminiscent of classical island biogeography theories, but different mechanisms may be responsible.

KEYWORDS

Assembly rules, island biogeography, HAUSGARTEN, megafauna, encrusting fauna, hard substrata
INTRODUCTION

Island fauna have been of interest to ecologists for many years because of the unique characteristics they possess: the contradictory phenomena of nanism and gigantism, and low species richness countered by high endemicity (Whittaker & Fernandez-Palacios 2007). The fauna and flora in island-like habitats have filled a substantial body of ecological literature, as an understanding of isolated habitats informs such wide-ranging problems as dispersal, succession and the design of natural reserves (Tjørve 2010).

Even though much of the island ecology literature centers on terrestrial habitats, the deep sea contains numerous isolated hard-bottom habitats (Young 2009) with high biodiversity that may function like islands. Island-like habitats at the deep sea floor range in size from landscape-scale features such as seamounts (Clark et al. 2010) and canyons (DeLeo et al. 2010) to isolated chemosynthetic communities at hydrothermal vents (Lutz & Kennish 1993), cold seeps (Sibuet & Olu 1998), sunken wood (Bienhold et al. 2013) and whale falls (Smith & Baco 2003), to small-scale structures such as manganese nodules (Mullineaux 1987), sea urchin tests (Hétérier et al. 2008) and sponge stalks (Beaulieu 2001).

In this image analysis, we focus on the isolated hard-bottom communities on dropstones in the Fram Strait. Dropstones are stones, here defined as anything larger than a pebble (Wentworth 1922), that are scraped up by glaciers, carried out to sea and released by melting icebergs. They constitute the most common hard substrata north of 45° N in the North Atlantic (Kidd et al. 1981). They are inhabited primarily by sessile, suspension-feeding invertebrates (Oschmann 1990, Schulz et al. 2010) and can serve as a “resting place” for motile fauna such as shrimps and amphipods. Dropstones increase habitat heterogeneity and
megafaunal diversity where they occur (MacDonald et al. 2010). The presence of a dropstone can also affect the surrounding meiofauna (Hasemann et al. 2013). Dropstones, like most other hard substrata in the deep sea (Young 2009) are essentially hard-substratum islands surrounded by a sea of mud.

Using image analysis, we quantify the biotic and abiotic factors structuring dropstone communities. Classical island theory (including MacArthur and Wilson’s equilibrium theory of island biogeography (MacArthur & Wilson 1967) and Diamond’s assembly rules (Diamond 1975)) have pointed to the influence of island size (Connor & McCoy 1979), proximity to a mainland (MacArthur & Wilson 1967), and interspecific competition (Diamond 1975) on insular fauna. Each of these classical theories has been criticized and modified since first publication (Connor & Simberloff 1979, Anderson & Wait 2001), filling a large body of literature even in recent years (Lomolino 2000, Gotelli 2001). In this analysis, we examine the effects of these classical factors on dropstone communities – size, proximity to a potential source population, and biotic interactions among the fauna. We also test for nested patterns of the fauna, which result when ever-smaller or ever-more-isolated habitats are inhabited by ever-smaller sub-sets of species, such that each sub-set is nested within the next-largest faunal sub-set. Nested patterns are common for terrestrial fauna and have implications for conservation (Tjørve 2010). We compare our results to patterns found in terrestrial island communities and discuss how our findings may enlighten current thought on other island-like habitats.
MATERIALS AND METHODS

Image collection

Images of the seafloor were recorded in July 2012, during expedition ARK XXVII/2 of German research icebreaker RV Polarstern, from five stations in the LTER (Long-Term Ecological Research) observatory HAUSGARTEN, in the eastern Fram Strait (Soltwedel et al. 2005). Four of the five stations (S3, HG IV, N3, N5) analysed represent soft-sediment sites and constitute a latitudinal transect along the 2500 m isobath, while the remaining station, here referred to as “Senke,” includes a steep deep-water rocky reef (Table 1, Fig. 1). However, at the Senke site, photographs included in the present image analysis were all recorded from the soft-sediment seafloor at the foot of the reef (Meyer et al. 2014). Dropstone densities along the latitudinal transect (S3, HG IV, N3) are not significantly different, but there are more pebbles at the northerly stations, corresponding to increased ice cover (Taylor et al. 2016). Bottom current in the study area is predominantly to the northwest (Meyer et al. 2014).

Images were recorded using a downward-facing towed camera system, the Ocean Floor Observation System (OFOS), and specifics are reported by Meyer et al. (2013) for 2012 sampling. The target altitude was 1.5 m, and each image shows approximately 3-4 m² of the seafloor. Three lasers were each mounted 52 cm apart on the camera frame to produce points in the photos that were used for size reference. Images were recorded automatically every 30 s, and additional manually-triggered images were recorded when objects of interest were observed. Each image was geo-referenced with a unique latitude and longitude.
Image analysis

Images that were unusually bright, unusually dark, or outside the most common range of altitudes (1.3 - 1.6 m) were considered ineligible for analysis. In order to calculate the density of stones at each station in 2012, 40 automatically-recorded images (which did not necessarily contain dropstones) were randomly sub-selected from the eligible images at each station, and the number of stones in each image was counted and divided by the image area to give stones m$^{-2}$. In order to assess the change in dropstones and pebble densities over time, 80 images were selected from eligible OFOS images at stations N3 and S3 in 2011-2015 (Taylor et al. 2016).

For the analysis of dropstone fauna, 40 automatically-recorded eligible images showing stones of any size were randomly sub-selected for each station. These stones observed in the automatic images were primarily of small size for every station except Senke; therefore, an additional 40 manually-triggered images containing large stones (large enough to be seen without zooming in on the image) were also randomly sub-selected from the eligible images for stations S3, HG IV, N3 and N5. Altogether, 541 images and 1677 individual stones were analyzed.

The surface area of each stone (as it was visible in the downward-facing images) was traced using the freehand selection tool and measured in ImageJ (NIH, USA). Megafauna present on each stone were counted and sorted into morphotypes. Some morphotypes could be identified by comparison of the images to Bergmann et al. (2011). For those morphotypes also observed on the rocky reef at station Senke, morphotype names in this study match the names used by Meyer et al. (2014).
**Data analysis**

In order to determine whether dropstones were randomly distributed on the seafloor, we tested if the frequency distribution of stone densities differed significantly from a Poisson distribution using a G-test in Biomstat v4 (Exeter Software, USA). A G-test was also used to determine if dropstone fauna were randomly distributed by comparing to a Poisson distribution. Changes in dropstone density over time were tested with ANOVA. Stones were sorted into size categories (<10, 11-20, 21-30...91-100, 101-150, 151-200, >200 cm² in downward-facing view) in order to construct frequency distributions of all available stones and stones inhabited by fauna; these frequency distributions were compared using a G-test. Linear and logarithmic regressions of the abundance, richness, evenness, and diversity of fauna against stone size and distance to the Senke rocky reef were constructed using Biomstat. The variables morphotype richness and stone area were each log-transformed to see whether dropstone communities showed the classical log-linear relationship between these variables (Connor & McCoy 1979). Correlations between the biotic community composition and other dropstone parameters (stone size, location, distance to the Senke rocky reef) were sought using Mantel tests in R (R Core Team 2013, Paradis et al. 2014).

In order to test for significantly nested patterns of the megafauna, we used the N₁ and BR indices in the software Nestedness (Ulrich 2006) according to the recommendation of Ulrich & Gotelli (2007) and a fixed-fixed null model to generate 95% confidence intervals of each index. Non-random patterns of species co-occurrence were sought for each station using the software EcoSim (Entsminger 2014). According to the recommendation of Gotelli (2000) for archipelago-like datasets, we used a fixed-fixed null model and the C-score index. To detect
pairwise non-random co-occurrence patterns in the megafauna, we used the software Pairs (Ulrich 2008), once again applying the C-score index of co-occurrence and a fixed-fixed null model. Bayes M criterion was used to assess significance of pairwise comparisons, following Gotelli & Ulrich (2010).

RESULTS
The physical environment
Dropstones had a clumped distribution on the seafloor. The frequency distribution of stone densities was skewed right and differed significantly from a Poisson distribution (G-test, $G = 326, p < 0.001$; Fig. 2) with a variance-to-mean ratio of 8.3. However, a test for spatial auto-correlation of stone density against distance to the Senke rocky reef indicated a significant negative correlation (Mantel test based on Euclidean distance matrices, $z = 2.6 \times 10^8$, $p = 0.001$), meaning that images the same distance from the Senke rocky reef had significantly dissimilar stone densities. In other words, clusters of stones were distributed on the seafloor without regard for distance from the rocky reef.

Dropstones and pebbles each had significantly higher density at station S3 in 2015 than in 2011-2013 (dropstones, ANOVA, $F = 3.39$, $p = 0.018$; pebbles, ANOVA, $F = 202.65$, $p < 0.001$; Fig. 3). At station N3, the density of dropstones was not significantly different among years (ANOVA, $p > 0.05$), but pebbles had higher density in later years (2013-2015) than in 2011-2012 (ANOVA, $F = 42.77$, $p < 0.001$; Fig. 3).

Most dropstones included in this study were small ($< 10 \text{ cm}^2$ surface area in downward-facing view), and the size distribution of all dropstones was skewed right (Fig. 4). Stone size was
not significantly spatially auto-correlated (Mantel test using Euclidean distance matrices based on stone size and latitude/longitude, \( z = 7.6 \times 10^7, p = 0.243 \)) and is also not significantly correlated to distance from the Senke rocky reef (Mantel text using Euclidean distance matrices, \( z = 3.8 \times 10^3, p = 0.963 \)). Therefore, the size of a dropstone is not related to its position on the seafloor, so stone size can be considered as an independent factor potentially influencing the biotic communities.

**Relationship of stone size to the biotic community**

Larger dropstones were inhabited by more individuals and had higher morphotype diversity. The number of individuals (\( N \)), species richness (\( S \)), Margalef richness (\( d \)), evenness (\( J' \)), and diversity (\( H' \)) of the fauna on a particular stone all showed a logarithmic relationship to the stone size (Fig. 5A-E). The relationship was strongest for \( H' \) (\( R^2 = 0.57 \)) and \( S \) (\( R^2 = 0.53 \)) and weakest for \( N \) (\( R^2 = 0.38 \)). A log-log transformation of the species-area plot is commonly reported for terrestrial islands (MacArthur & Wilson 1967, Rusterholz & Howe 1979), and a similar transformation of the dropstone data also revealed a strong log-log relationship of species richness and stone area (\( R^2 = 0.52 \); Fig. 5F).

Even though most available dropstones were small, the dropstone fauna primarily inhabited larger stones (Fig. 4). The size-frequency distribution of stones inhabited by fauna was skewed left, differing significantly from the right-skewed size-frequency distribution of all available stones (G-test, \( G = 4.3 \times 10^3, p < 0.001 \)). However, the size-frequency distribution of inhabited stones varied for different morphotypes (Heterogeneity \( G = 1.5 \times 10^3, p < 0.001 \)). The vast majority of morphotypes (37 of 56) were found primarily on larger stones (G-test, \( p < 0.05 \);
Table 1), but 19 of the 56 morphotypes had a distribution not significantly different from the size distributions of all available stones (G-test $p > 0.05$; Table S1). These 19 morphotypes were generally rare, however, being observed 21 or fewer times on a total of 1677 dropstones examined. Despite the higher diversity observed on larger stones, there was not a significant correlation between the composition of the biotic community (represented in a Bray-Curtis similarity matrix) and the size of the stone (Euclidean distance matrix) (Mantel test, $z = 8.8 \times 10^8$, $p = 0.469$). In other words, stones of the same size did not necessarily have similar faunal composition.

**Relationship of dropstone distribution to the biotic community**

Dropstone fauna had an overdispersed (clumped) distribution. The frequency-distribution of $N$ (number of individuals on a stone) differed significantly from a Poisson distribution ($G$-test, $G = 1.5 \times 10^4$, $p < 0.001$; Fig. 6), with a variance-to-mean ratio of 87.8. This was the case for every morphotype (heterogeneity $G = 0$, $p = 1$). A significant spatial auto-correlation was found for dropstone faunal composition (Mantel test using Bray-Curtis similarity matrix based on the biotic data and Euclidean distance matrix based on latitude/longitude, $z = 4.3 \times 10^6$, $p = 0.001$), meaning that stones closer to one another in space had more similar biotic communities. A similar test of the biotic data against the distance to the Senke rocky reef also showed a significant correlation ($z = 1.9 \times 10^8$, $p = 0.001$), meaning that stones located the same distance from the Senke rocky reef had more similar communities. Even when a presence-absence transformation of the biotic data was used, a significant spatial
auto-correlation was found (Mantel test using lat/long, $z = 5.5 \times 10^6$, $p = 0.001$; Mantel test using distance to the reef, $z = 2.4 \times 10^8$, $p < 0.001$), which means that differences in the biotic communities in different parts of the study area were due to the presence or absence of morphotypes and not just their relative abundances.

The highest richness, abundance, evenness, and diversity of dropstone fauna was found at station Senke, located at the foot of the rocky reef. A range of values was found at each station, though greater maximum values for richness, abundance, and diversity were found at stations closer to the reef. Abundance, richness, evenness, and diversity each showed a significant negative linear regression to distance from the rocky reef (Fig. 7).

Dropstone fauna showed no evidence of a nested distribution among stations. The $N_1$ (52) and BR (32) indices both fell within the 95% confidence interval ranges (39-53 and 32-38, respectively).

Interactions between morphotypes

The data revealed patterns of non-random co-occurrence at three of the five stations: Senke, HG IV and N3 ($C > e$, $p < 0.001$). No significant non-random co-occurrence patterns were found for stations N5 and S3 ($p = 0.12$ and 0.09, respectively).

Pairwise tests showed only a small number of non-randomly co-occurring morphotype pairs at each station (Table 2). A total of 12 morphotype pairs (of 1540 possible pairs) at four stations were found to co-occur less often than expected by random chance. An additional eight pairs of morphotypes at three stations were found to non-randomly co-occur more often than expected by random chance (Table 2).
DISCUSSION

The physical environment

The clumped distribution of dropstones probably reflects their origin in icebergs. A single iceberg may have carried many stones accumulated in clumps, which were released at the same time as the iceberg melted. In addition, the clusters are distributed randomly, without respect to the rocky reef. There is the potential for some stones to have broken off from the rocky reef and rolled down the adjacent slope (Meyer et al. 2014); however, it does not appear that this is the primary force affecting the distribution of dropstones.

The size and location of dropstones correlated with the biotic community, with higher richness, abundance, and diversity of fauna on larger stones, and a significant spatial auto-correlation demonstrated with respect to the rocky reef. The fact that these two factors, stone size and proximity to the reef, both independently and significantly impacted the biotic community is reminiscent of MacArthur and Wilson's classical island biogeography theory, which pointed to the influence of island area and distance from a source population on island fauna (MacArthur & Wilson 1967). Even though the observable patterns in dropstone communities resemble classical islands, the mechanisms driving these patterns may not be the same as have been suggested for classical islands or habitat islands. The possible mechanisms structuring dropstone communities are discussed in more detail below.

Relationship of stone size to the biotic community

Our results showed higher species richness on larger stones; common morphotypes were also more often found on larger stones. Dropstone fauna may thrive on larger stones
because of elevated food supply. Larger stones extend higher in the benthic boundary layer, 
where they are exposed to faster currents that bring particulate food for suspension feeding 
(Vogel 1996). Suspension feeders are well-known to inhabit elevated substrata on seamounts 
(Clark et al. 2010) and fjord sills (Mortensen et al. 2001), and on a smaller scale, suspension- 
feeding foraminifera inhabit glass sponge stalks (Beaulieu 2001) and manganese nodules 
(Mullineaux 1988). Dropstone megafauna may gain an advantage for suspension feeding by 
inhabiting larger stones (Schulz et al. 2010).

Larger dropstones may be older, as they would take longer to be covered by 
sedimentation. This means it is possible that the older stones have higher diversity, abundance, 
and richness of fauna because they have been underwater for longer and therefore harbor 
communities in a state of more advanced succession. However, this explanation ignores the 
fact that new dropstones are being deposited in the study area in modern times. All stations 
except S3 are seasonally covered by sea ice. Glaciers in west Svalbard fjords have been known 
to calve icebergs carrying terrestrial material in modern times (Hagen et al. 2003), and ice is 
also advected into the Fram Strait from the Laptev and Kara seas (Bergmann, unpubl. data). Our 
data from S3 and N3 show an increase in pebbles on the seafloor from 2011-2015 (Fig. 3), and 
both dropstone and hard substratum density increased significantly at HG IV between 2002 and 
2011 (Bergmann, unpubl. data).

On terrestrial islands, habitat diversity, disturbance level and primary productivity are all 
correlated with island size and have been put forth as explanations for the higher richness of 
fauna on larger islands (Gotelli & Graves 1996). However, these factors probably have very little 
effect on dropstone communities. Habitat is the rock surface, primary production does not
occur locally, and physical disturbance is also relatively rare compared to terrestrial islands (though predators may be a source of disturbance on dropstones). Based on our data, we cannot exclude the “passive sampling” hypothesis (Gotelli & Graves 1996) as an explanation for the higher richness and abundance of fauna on larger stones. This hypothesis states that larger islands (stones) are colonized by more organisms simply because they are larger targets for dispersing propagules. Larger stones are also exposed to faster bottom currents, where the larval flux is probably greater. We find the “passive sampling” hypothesis and its corollary of greater larval supply on larger stones to be the most parsimonious explanation for the higher abundance, morphotype richness, and diversity on larger dropstones.

It should be especially noted that there was no significant correlation between the size of dropstones and the composition of the biotic communities inhabiting them. This means that there is not one community of organisms inhabiting smaller stones and a separate community inhabiting larger stones, as was suggested by Diamond (1975) for avifauna on terrestrial islands. Instead, the morphotypes present on each stone are a random sub-set of the available morphotypes, and the fauna on larger stones happen to be more diverse because they are a larger sub-sample of the available fauna.

The relationships between biotic parameters (N, S, d, J’, H’) and the size of a stone were all asymptotic, so an infinitely large stone would not be able to host an infinitely large number of individuals or species. This asymptotic relationship may indicate that there is a maximum carrying capacity for a stone (asymptotic relationship to N) or that there is a finite pool of morphotypes from which these individuals can be drawn (asymptotic relationship to S, morphotype richness). The mathematical relationship between morphotype richness and stone
area was linear when each of these variables was log-transformed; a pattern commonly found in classical island literature (MacArthur & Wilson 1967). Therefore, it is possible that this often-discussed classical pattern is merely the result of species on a particular island or habitat island being a sub-sample from a finite pool of available species.

Thus, if the fauna on a stone is considered a sub-sample of the available finite pool of morphotypes, logic dictates that a sufficiently large stone should host the majority or even all of the available morphotypes, and the faunal communities would begin to converge, showing greater similarity at larger stone sizes. However, this is not observed to be the case for dropstone communities, as there was no correlation between stone size and biotic community composition. It is possible that the stones in the present study are simply not large enough to host all available morphotypes of fauna; the maximum morphotype richness on a single stone was 26, less than half of the 56 morphotypes available morphotypes found on all dropstones.

Habitat diversity, disturbance, primary productivity, and age of the stones do not offer satisfactory explanations for the higher richness, abundance, and diversity of fauna on larger stones. We find the most parsimonious explanation to include the “passive sampling” hypothesis (that larger stones are larger targets for competent larvae) and its hydrodynamic corollaries (that larger stones are exposed to faster current, bringing increased larval supply and particulate food).

**Relationship of dropstone distribution to the biotic community**

Dropstone fauna were spatially auto-correlated and had a clumped distribution, which may be a result of dispersal via a planktonic larval stage. Following a reproductive event, larvae
of the dropstone fauna disperse and settle on surrounding stones, resulting in the observed
clumped distribution of morphotypes. It is unknown how long dropstone fauna persist as larvae
in the water column or how far they disperse; however, the dropstone fauna consist of mostly
encrusting species, which generally tend to have short-lived larvae (Jackson 1986). Short pelagic
larval duration would restrict the dispersal of dropstone fauna to the stones in a small area
surrounding natal stones, resulting in a clumped distribution. Connectivity among stones via
larval dispersal is a key difference between dropstone communities and classical island or
habitat island studies; namely, dropstone fauna disperse among stones and may have a much
greater degree of connectivity than birds or mammals that self-recruit to the same island or
habitat island over many generations.

A spatial auto-correlation for dropstone fauna was also found with respect to the rocky
reef; in other words, stones located the same distance from the reef had more similar
communities. The rocky reef has the potential to serve as a source population for hard-bottom
fauna on dropstones, given its dense populations of sessile fauna and its upstream location
from 4 of the 5 dropstone stations in this study (Meyer et al. 2014). It indeed appears that
increased larval supply from the rocky reef may affect dropstone communities, based on the
higher abundance, richness, and diversity of fauna found on stones nearer to the reef (Fig. 7).
However, we cannot conclude that the rocky reef is the sole or even the primary source of
larvae to the dropstones. If this were the case, one would also expect a nested pattern of the
fauna, in which the most morphotypes would be present nearer the reef (at station Senke), and
nested sub-sets of the fauna would be present at stations further away from the reef. However,
our data showed no evidence of nestedness among stations. In fact, dropstones at station S3,
south of the reef, featured fauna not significantly different in abundance, richness, and diversity from station HG IV, located equidistant but upstream of the reef (Fig. 7).

In some cases, hard-bottom fauna dispersing to widely-spaced substrata may have to delay metamorphosis (Marshall & Keough 2003), which may affect colony growth or recruits’ performance as adults (Marshall & Keough 2004). However, we have no reason to believe that hard-bottom fauna on dropstones would be incapable of reproducing and therefore reliant on the rocky reef as a source of larvae. It is more likely that larvae disperse from both colonized dropstones and the densely-populated reef, resulting in the patterns observed in our data: clumped distribution of dropstone fauna, and higher abundance, richness, and diversity of fauna closer to the rocky reef.

Interactions between morphotypes

We found evidence of non-random co-occurrence patterns at three of five stations. For those pairs co-occurring less often than expected by random chance, it cannot necessarily be concluded that competitive exclusion is the cause, as is traditionally concluded for terrestrial islands (Diamond 1975). Many dropstone morphotypes are encrusting forms – sponges, ascidians, or bryozoans. In fact, nine of the twelve morphotype pairs found to non-randomly co-occur less often than expected by chance included at least one encrusting form. If these encrusting morphotypes were truly competing, we would expect them to occupy larger portions of the dropstone surface area and even overgrow each other, such as is commonly observed for competing encrusting species in shallow water environments (Sebens 1986, Oschmann 1990). In no case were encrusting dropstone species observed to overgrow one
another, and in fact large portions of the available space on dropstones were left uncolonized (Meyer, pers. obs., Oschmann 1990). While it is possible that already-established fauna on a stone may consume larvae of potentially-settling species, experimental evidence from shallow water has shown larval predation does not always significantly affect recruitment (Young & Gotelli 1988, Young 1989, Young & Cameron 1989).

Rather than competitive exclusion, pairs of morphotypes may non-randomly co-occur on dropstones as a result of their own distribution. A significant spatial auto-correlation was found for the dropstone fauna, even when a presence-absence transformation of the biotic data was used, indicating that the absence of some morphotypes from parts of the study area leads to the observed patterns in the biotic data. Dropstone fauna also had a clumped distribution. If two species occur in different parts of the study area or are most abundant in different parts of a particular station, they would seldom be found together. It is not necessary to invoke interspecific competition to explain non-random co-occurrence of dropstone fauna; the observed patterns may just be a result of the clumped distribution of fauna.

We also found that eight morphotype pairs co-occurred more often than expected by random chance. For example, “Hormathiidae” (Fig. S4B) and Cladorhiza cf. gelida (Fig. S1I) were found to co-occur more often than expected by chance at stations S3 and N5. Large erect species such as C. cf. gelida and Caulophacus arcticus (Fig. S1B) were commonly observed in the images being surrounded by mobile crustaceans including Bythocaris cf. leucopis (Fig. S5A) and “amphipod” (Fig. S5E). Individuals of C. cf. gelida also in many cases had one or more anemones, “Hormathiidae,” living on them (Fig. 8). We find it likely that these epibiotic species take advantage of the elevated structure provided by large structural basibionts. A number of
species live on or are associated with large structural coral species in the deep sea (Cordes et al. 2008), and deep-sea suspension feeders climb on stones, sponges, or the spines of sea urchins to elevate themselves off the seafloor and expose themselves to better currents (Gutt & Schickan 1998). “Hormathiidae” is very likely elevating itself for suspension feeding by living atop C. cf. gelida, and it also inhabits stalks of the crinoid Bathycrinus carpenterii [Fig. S6B; Bergmann, unpubl. data]. Similar epibiotic relationships have been found for Antarctic fauna and are mostly likely commensal (Gutt & Schickan 1998). Morphotypes that utilized large structural basibionts were also found to co-occur more often than expected by chance (“Hormathiidae” – B. cf. leucopsis at stations S3 and N5, Poliometra prolixa – B. cf. leucopsis and Poliometra prolixa – “amphipod” at HG IV). It is not entirely clear what advantage B. cf. leucopsis and the amphipod gain by resting on large sponges, though they may be protected from predators or gain some advantage in feeding.

Other pairs of species co-occurred more often than expected, though the reason is not so obvious. In the case of “lobe-like sponge” (Fig. S2D) and “pycnogonid” (Fig. S5C) at S3, perhaps one is the prey of the other. For the pair Polymastia sp. (Fig.S2B) – “white pancake sponge” (Fig. S3C) at HG IV, we are unable to conjecture a reason. Our results demonstrate that some morphotype pairs co-occur more often than expected by random chance and that commensalism can be the basis for non-random species co-occurrence patterns.

Conclusion

Dropstones constitute island-like habitats for hard-bottom fauna at high latitude. While the patterns observed in dropstone communities bear some resemblance to classical island
systems, the mechanisms causing these patterns are not necessarily the same. Differences in primary productivity, habitat diversity, and physical disturbance are not satisfactory explanations for the distributions of dropstone fauna; rather, simple mechanisms such as hydrodynamics and larval dispersal offer parsimonious explanations. This study is to our knowledge the first time a facilitation mechanism (commensalism) has been shown to drive non-random co-occurrence patterns in island-like fauna. An understanding of dropstone communities provides new insights for studies in other island-like habitats.

ACKNOWLEDGEMENTS

We thank the officers and crew of R/V Polarstern for their assistance at sea. Dorte Janussen (sponges, Senckenberg Museum of Natural History), Andrey Vedenin (crustaceans, echinoderms, P.P. Shirshov Institute of Oceanology), Leen van Ofwegen (cnidarians, National Museum of Natural History), Estefania Rodriguez (cnidarians, American Museum of Natural History) kindly identified species from voucher specimens or photos. Nicholas Gotelli (University of Vermont) and Frances White (University of Oregon) provided statistical guidance. Comments from Michelle Wood and Alan Shanks (University of Oregon) and _ reviewers improved earlier versions of this manuscript. This material is based upon work supported by the National Science Foundation Graduate Research Fellowship Program under Grant No. DGE-0829517. MB was funded by the Helmholtz Alliance ROBEX (Robotic Exploration of Extreme Environments). This study contributes to the tasks of the Helmholtz-funded program FRAM (Frontiers in Arctic Marine Research) and has Eprint ID 37698 of the Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung, Germany.
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Fig. 1. Map of stations in the HAUSGARTEN observatory where dropstone images were recorded. Depth contours are shown every 250 m.

Fig. 2. Frequency distribution of stone densities in 40 randomly sub-selected images from each station, and a Poisson distribution with the same mean. A significant difference between the two distributions (see text) indicates a clumped distribution of dropstones in the study area.

Fig. 3. A, density (m$^{-2}$) of dropstones; B, density of pebbles at stations N3 and S3 in the HAUSGARTEN observatory, 2011-2015. Error bars show 95% confidence intervals; error bars for pebbles at S3 are small enough to not be visible.

Fig. 4. Size-frequency distribution of all available dropstones, and a size-frequency distribution of inhabited dropstones. A significant difference between the two distributions (see text) indicates that dropstone fauna primarily inhabit larger stones.

Fig. 5. Frequency distribution of the number of individuals on a dropstone (N), and a Poisson distribution with the same mean. A significant difference between the two distributions (see text) indicates that dropstone fauna have a clumped distribution.

Fig. 6. A-E, biotic parameters (abundance, richness, evenness, and diversity of fauna) on a dropstone versus the size (surface area visible in downward-facing view); F, morphotype richness on a dropstone versus the size of the stone, with each axis log(x+1)-transformed to show the log-linear species-area relationship common among island systems in the classical literature.

Fig. 7. Biotic parameters (abundance, richness, evenness, and diversity of fauna) on dropstones versus distance to the foot of the Senke rocky reef. Linear regressions shown.
Fig. 8. A, Crustaceans including *Bythocaris* cf. *leucopsis* and "amphipod" resting on *Caulophacus arcticus*; B, *Poliometra prolixa* (white arrow) and *B. cf. leucopsis* on *C. arcticus*; C, "Hormathiidae" as an epibiont on *Cladorhiza cf. gelida*.
Table 1. Summary of Ocean Floor Observation System (OFOS) deployments during ARK XXVII/2.

<table>
<thead>
<tr>
<th>Photographic transect no.</th>
<th>Station</th>
<th>Date</th>
<th>Start latitude (N)</th>
<th>Start longitude (E)</th>
<th>Start depth (m)</th>
<th>End latitude (N)</th>
<th>End longitude (E)</th>
<th>End depth (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>PS80/176-1</td>
<td>S3</td>
<td>19-Jul-2012</td>
<td>78° 37.04′</td>
<td>5° 00.07′</td>
<td>2360</td>
<td>78° 37.00′</td>
<td>5° 8.56′</td>
<td>2352</td>
</tr>
<tr>
<td>PS80/179-3</td>
<td>HG IV</td>
<td>21-Jul-2012</td>
<td>79° 01.98′</td>
<td>4° 09.75′</td>
<td>2630</td>
<td>79° 03.88′</td>
<td>4° 17.18′</td>
<td>2409</td>
</tr>
<tr>
<td>PS80/186-5</td>
<td>N5</td>
<td>24-Jul-2012</td>
<td>79° 56.07′</td>
<td>3° 07.98′</td>
<td>2534</td>
<td>79° 55.63′</td>
<td>3° 05.69′</td>
<td>2554</td>
</tr>
<tr>
<td>PS80/193-1</td>
<td>N3</td>
<td>26-Jul-2012</td>
<td>79° 36.04′</td>
<td>5° 09.88′</td>
<td>2748</td>
<td>79° 33.53′</td>
<td>5° 16.99′</td>
<td>2608</td>
</tr>
<tr>
<td>PS80/196-1</td>
<td>Senke</td>
<td>27-Jul-2012</td>
<td>79° 05.98′</td>
<td>4° 23.01′</td>
<td>2296</td>
<td>79° 06.02′</td>
<td>4° 33.92′</td>
<td>2041</td>
</tr>
</tbody>
</table>
Table 2. Morphotype pairs at each station that co-occur more or less often than expected by random chance.

<table>
<thead>
<tr>
<th>Station</th>
<th>Morphotype 1</th>
<th>Morphotype 2</th>
<th>Less or more often than by chance?</th>
</tr>
</thead>
<tbody>
<tr>
<td>S3</td>
<td>Gray encrusting sponge 1</td>
<td>Myxilliniid sponge</td>
<td>Less</td>
</tr>
<tr>
<td>S3</td>
<td>Gray encrusting sponge 1</td>
<td>Puffy white encrustment</td>
<td>Less</td>
</tr>
<tr>
<td>S3</td>
<td>Bathypellia margaritacea</td>
<td>Gray dome sponge</td>
<td>Less</td>
</tr>
<tr>
<td>S3</td>
<td>Bathypellia margaritacea</td>
<td>Myxilliniid sponge</td>
<td>Less</td>
</tr>
<tr>
<td>S3</td>
<td>Hormathiidae</td>
<td>Bythocaris cf. leucopis</td>
<td>More</td>
</tr>
<tr>
<td>S3</td>
<td>Hormathiidae</td>
<td>Cladorhiza cf. gelida</td>
<td>More</td>
</tr>
<tr>
<td>S3</td>
<td>Lobe-like sponge</td>
<td>Pycnogonid</td>
<td>More</td>
</tr>
<tr>
<td>HG IV</td>
<td>Bathypellia margaritacea</td>
<td>Poliometra prolixa</td>
<td>Less</td>
</tr>
<tr>
<td>HG IV</td>
<td>Bathypellia margaritacea</td>
<td>Lobe-like sponge</td>
<td>Less</td>
</tr>
<tr>
<td>HG IV</td>
<td>Bathypellia margaritacea</td>
<td>Gersemia fruticoso</td>
<td>Less</td>
</tr>
<tr>
<td>HG IV</td>
<td>Polymastia sp.</td>
<td>White pancake sponge</td>
<td>More</td>
</tr>
<tr>
<td>HG IV</td>
<td>Poliometra prolixa</td>
<td>Bythocaris cf. leucopis</td>
<td>More</td>
</tr>
<tr>
<td>HG IV</td>
<td>Poliometra prolixa</td>
<td>Amphipod</td>
<td>More</td>
</tr>
<tr>
<td>Senke</td>
<td>Yellow encrusting sponge</td>
<td>Phakellia sp.</td>
<td>Less</td>
</tr>
<tr>
<td>Senke</td>
<td>Asymmetrical white sponge</td>
<td>Gray encrusting sponge 1</td>
<td>Less</td>
</tr>
<tr>
<td>N5</td>
<td>Myxilliniid sponge</td>
<td>Gray encrusting sponge 1</td>
<td>Less</td>
</tr>
<tr>
<td>N5</td>
<td>Bathypellia margaritacea</td>
<td>Myxilliniid sponge</td>
<td>Less</td>
</tr>
<tr>
<td>N5</td>
<td>Gray encrusting sponge 1</td>
<td>Puffy white encrustment</td>
<td>Less</td>
</tr>
<tr>
<td>N5</td>
<td>Hormathiidae</td>
<td>Bythocaris cf. leucopis</td>
<td>More</td>
</tr>
<tr>
<td>N5</td>
<td>Hormathiidae</td>
<td>Cladorhiza cf. gelida</td>
<td>More</td>
</tr>
</tbody>
</table>
Fig. 2

- Observed distribution
- Poisson distribution

No. images vs. Stone density (m$^2$)
Fig. 3

(A) Dropstones m<sup>2</sup>

(B) Pebbles m<sup>2</sup>

Year:
- 2010
- 2011
- 2012
- 2013
- 2014
- 2015
Fig. 4

No. stones

Stone size (cm³)

- All available stones
- Inhabited stones

[Bar chart showing distribution of stone sizes with categories from <10 to >200 cm³]
Fig. 5

A

\[ y = 3.4383 \ln(x) - 4.8542 \]
\[ R^2 = 0.3791 \]

B

\[ y = 1.3769 \ln(x) - 1.3648 \]
\[ R^2 = 0.5325 \]

C

\[ y = 0.4775 \ln(x) - 0.4707 \]
\[ R^2 = 0.517 \]

D

\[ y = 0.2053 \ln(x) - 0.1256 \]
\[ R^2 = 0.4213 \]

E

\[ y = 0.3524 \ln(x) - 0.3793 \]
\[ R^2 = 0.5739 \]

F

\[ y = 0.3359x \]
\[ R^2 = 0.5294 \]
Fig. 6

- Observed distribution
- Poisson distribution

No. individuals on stone (N)
Fig. 7

A. No. of individuals (N)

\[
y = -0.044x + 5.1854 \quad p < 0.001
\]

B. Morphotype richness (S)

\[
y = -0.0202x + 2.7246 \quad p < 0.001
\]

C. Margalef richness (d)

\[
y = -0.008x + 0.9756 \quad p < 0.001
\]

D. Pielou evenness (J)

\[
y = -0.0037x + 0.5027 \quad p < 0.001
\]

E. Shannon-Wiener diversity (H')

\[
y = -0.0055x + 0.6761 \quad p < 0.001
\]

Distance from Senke rocky reef (km)