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# Abundance-Occupancy Relationships in Deep Sea Wood Fall Communities

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## Abstract

The generally positive relationship between the number of sites a species occupies and its average abundance within those sites provides an important link between population processes occurring at different spatial scales. Although such Abundance-Occupancy Relationships (AORs) have been documented across a very wide range of taxa and in many different environments, little is known of such patterns in Earth's largest ecosystem, the deep sea. Wood falls—derived from natural or anthropogenic inputs of wood into the oceans—constitute an important deep-sea habitat, habouring their own unique communities ultimately entirely dependent on the wood for chemical energy. In this study we take advantage of the unique features of an experimental wood fall deployment to examine AORs for the first time in deep-sea invertebrates. The study design combines advantages of both experimental (tractability, control of key environmental parameters) and observational (natural colonisation by taxonomically diverse communities) studies. We show that the interspecific AOR is strongly positive across the 48 species occurring over 32 wood fall communities. The precise form of the AOR is mediated by both species-level life history (body size) and by the colonisation stage at which communities were harvested, but not by environmental energy (wood fall size). Temporal dynamics within species are also generally consistent with positive intraspecific AORs. This support for positive AORs in the deep sea is an important extension of a macroecological generality into a new environment offering considerable potential for further testing and developing mechanistic macroecological theories.

## Introduction

Knowing where species occur, and in what numbers, is fundamental to many questions in ecology. Macroecologists have long known that these two key variables are not independent of each other: the number of sites a species occupies and the abundance it reaches within those sites (and, by extension, its total population size) are typically positively associated. Such Abundance Occupancy Relationships (AORs) are among the most general patterns in ecology, observed both across assemblages of species (the interspecific AOR) and within individual species through time (the intraspecific AOR), in numerous taxonomic groups and diverse habitats (Gaston et al. 2000, Blackburn et al. 2006, Borregaard and Rahbek 2010). AORs have attracted so much attention because they provide important links between local and regional scale population ecology, and between processes occurring within and between species (Freckleton et al. 2005, Webb et al. 2007); and because they imply that changes in local abundance can have disproportionate effects on regional occupancy, with important consequences for conservation (Lawton 1995, Freckleton et al. 2005). Understanding variation in the form and strength of AORs, and quantifying their dynamics in space and time, is likely therefore to provide useful insights into both fundamental ecological processes and into macroecological responses to environmental change (Holt and Gaston 2003, Webb et al. 2007, Fisher et al. 2010).

In particular, different forms and dynamics of AORs might be implied by different ecological mechanisms (e.g. Borregaard and Rahbek 2010), and simple considerations of regional-scale population dynamics have suggested that colonisation (itself determined both by species-specific traits and the distribution of suitable habitat) is key to AORs (Freckleton et al. 2005, 2006). This in turn predicts that AORs should vary systematically across groups of species differing in key traits as well as across contrasting environmental settings. For instance, if dispersal ability increases either directly or indirectly (e.g. through its effects on propagule size or number) with body size (Jenkins et al. 2007, Rundle et al. 2009, McClain in rev), then larger-bodied species should conform most closely to a pure colonisation model (i.e., all available habitat is colonised) and so have steeper relationships between abundance and occupancy than smaller species (Buckley and Freckleton 2010). On the other hand, low levels of environmental energy should lead to species responding more slowly to changes in habitat availability, because population local sizes are unable to increase rapidly, and such slow responses are expected to weaken AORs (Buckley and Freckleton 2010). Equally, lower levels of environmental energy (which can equivalently be expressed as a reduced amount of suitable habitat with sufficient resources for a population to persist) should also generally decrease species abundances on individual logs, increase patch-level extinctions, and decrease the likelihood of colonisation potential (and reduce connectivity) between logs (Holt et al. 2004, Freckleton et al. 2006, O'Sullivan et al. 2014). The consequent effects on the AOR may be complex, however. For instance, even if all species were identical in other relevant factors such as colonisation ability, weak AORs may result from both highly unconnected sets of patches low in resources, because densities are typically too low for persistence within patches {Freckleton:2006vh}. Equally, at higher resource levels, species-abundance distributions may be more equitable {Passy:2016kt}, leading to less variance in abundance across the community and less power to detect AORs - most likely because when patches are both highly connected and high in resources most species can attain sufficiently high densities within patches to persist and can reach most available patches (Freckleton et al. 2006).

Although these predictions are relatively simple to state, testing them has proved difficult even in the best-studied communities, which are typically limited in both taxonomic and functional diversity (see Webb et al. 2009). Nonetheless, various approaches to quantifying variability in AORs have yielded useful insights. For instance, meta-analyses have revealed broad differences in AORs across different kinds of communities or in different environmental settings (e.g. Blackburn et al. 2006). Targeted comparative studies have further explored variation around interspecific AORs, or different forms of intraspecific AORs, in terms of the life history and ecological characteristics of component species (e.g. {Holt:2003tk, Webb:2009jw, Buckley:2010cd, Bulafu:2015ie, Foggo:2007kb}. Finally, more controlled manipulations of both species composition and environmental variables in experimental settings, for instance using microcosms, have explicitly tested for effects of resource availability and wider ecological context (Holt et al. 2002, 2004). Taken together, these approaches support a role for biological traits associated with dispersal and colonisation (e.g. body size, reproductive mode) and habitat characteristics at both broad (e.g. marine v terrestrial) and finer scales (e.g. heterogeneity in resource availability) in mediating AORs. However, more robust insights could be gained by combining the control of experimental studies with the natural colonisation and community assembly of more observational studies of natural systems.

Deep-sea, wood-fall communities provide one setting in which such an approach is possible. Globally wood is transported in vast quantities to the oceans via rivers, and after drifting and becoming saturated with water, eventually sinks to the ocean floor (Wolff 1979, McClain and Barry 2014). On the deep-sea floor, wood falls develop largely endemic and highly diverse communities consisting of wood and sulfide obligates, and predators upon them (Voight 2007, McClain and Barry 2014, McClain et al. 2016). Experimentally placed deep-sea wood falls have high potential for testing predictions about AORs for several reasons. First, because the distinctive communities developing on wood falls are dependent on ephemeral and spatially unpredictable resources, they are typically made up of strong colonisers. Populations of many species are establised within one-two years (McClain and Barry 2014). Thus, natural colonisation processes are expected to lead to the establishment of AORs similar to those that would be observed in an unmanipulated system on experimentally tractable timescales (*c.* 5y). Second, communities developing on individual logs are clearly distinct from surrounding deep-sea sediment communities (McClain et al. 2016) and also appear to be largely independent of each other, in terms of community composition, even over quite small spatial scales (McClain and Barry 2014), although connectivity between them increases over time (McClain et al. 2016). This means that effectively macroecological studies—i.e., including multiple communities—can be conducted at experimentally tractable spatial scales (*c.* 500m$^2$).

Third, because invertebrate communities on wood falls rely on the wood that they colonise for energy (Bienhold et al. 2013, McClain et al. 2016), the total level of resource available to a community can be manipulated by varying the size of individual wood falls (McClain et al. 2016), in much the same way that resource availability to specific communities can be manipulated in microcosm experiments (e.g. Holt et al. 2004). Finally, collection and complete enumeration of entire communities (or a very close approximation thereof) from all available suitable habitat in the sampling region is possible (Voight 2007, McClain and Barry 2014, McClain et al. 2016). This ensures that any characteristics of the observed AORs cannot be attributed to sampling artefacts. Furthermore, communities can be collected at different points in time to assess how AORs develop with community successional stage.

Here, we fit AORs to deep-sea, wood-fall communities which had developed on 32 experimentally deployed logs for between 5 and 7 years. This is the first time that AORs have been quantified for these communities, and is among the first studies of the links between abundance and occupancy in the deep sea. We use the unique characteristics of deep-sea, wood-fall communities in general, and of the experimental deployment of wood falls in particular, to test whether AORs are mediated by resource availability (i.e. on small versus large individual wood falls). We predict higher population sizes on large logs, and higher connectedness between them, but because of the details of the experimental deployment (see below) and the expected complexities of the relationship between resource availability and the AOR (Freckleton et al. 2006), we do not have an a priori prediction of the effect of log size on the AOR (table 1). We also tested whether AORs are mediated by species mean body size, with the expectation that larger species are more likely to disperse between communities and so will exhibit more steeply positive AORs (table 1). Finally, we tested whether AORs differ between communities collected after 5 years compared to those collected after 7 years. We term this collection date variable 'colonisation stage'. Because we expect connectivity between communities to increase with time (McClain and Barry 2014), enhancing opportunities for colonisation between logs as resident populations mature and reproduce, we predict that AORs will be steeper, and/or will have a higher intercept (i.e. higher occupancy for a given density) in the longer-established set of communities (table 1). Conversely, the removal of communities at CS1 may lead to greater isolation between communities at CS2, but empirical data on community similarities through time do not support this {McClain:2014em}. Although the predicted effects of dispersal and connectivity are the same (table 1), we can distinguish between them by using independent proxies (body size and colonisation stage respectively).

## Methods

### *Study System*

The full protocol used for deployment and recovery of experimental wood falls is described in McClain et al. (2016). Briefly, using the Monterey Bay Aquarium Research Institute's Remotely Operated Vehicle (ROV) Doc Ricketts aboard the RV Western Flyer, 32 *Acacia* sp. logs were deployed at 3203 m in the Northeast Pacific Ocean (Station Deadwood: 36.154098° N, 122.40852° W) in November 2006, over a ~160m$^2$ area with ~5 meters between wood falls in 4 rows 10 m apart from one another (figure S1). Each log was sewn into a synthetic fiber mesh bag which did not hinder larval settlement but allowed for collection at the end of the experiment (Voight 2007). During ROV retrieval, logs were further sealed into 300 μm mesh bags with sealable closing lids, ensuring no loss of individuals and/or cross contamination among different samples. A complete enumeration of each wood fall community was obtained by picking all specimens from wood, and preserving them in either 95% ethanol or formalin. All of the taxa were identified to the species level except *Actinaria* spp, and species names were assigned to all taxa were possible. The final dataset is composed of 13169 individuals and 48 species (from 5 Phyla and 8 Classes). Almost all of these species are mobile as adults, i.e. capable of movement within individual logs, although we expect dispersal of adults across the *c.* 3-4m of inhospitable habitat between logs to be rare.

### *Environmental Energy*

Invertebrate communities assembling on wood falls rely on the wood that they colonise for energy (Bienhold et al. 2013, McClain et al. 2016). In this study, this environmental energy level was manipulated by using *Acacia* logs ranging in size from 0.6 to 20.6 kg. The experimental design was such that the distribution of log size was discontinuous, with 13 small logs (≤2.5kg) and 19 large logs (≥4kg). We use this to test whether AORs differ in the set of communities occurring on small logs (low availability of environmental energy; 2286 individuals, 40 species) compared to those on large logs (higher energy availability; 10883 individuals, 39 species).

### *Body size*

The combined total wet weight of all individuals of each species on each log was measured, which enabled the mean size of each species to be calculated by dividing through by abundance. This allowed us to test whether body size influences the strength or shape of the interspecific AOR in wood fall communities. Body size measures were not available for 9 of the 48 species due to poor condition of preserved specimens or too few individuals.

### *Colonisation Stage*

The 32 logs were collected in two stages, with 16 logs collected in October 2011 (Colonisation Stage 1, CS1, 5 years post-deployment) and the remaining 16 logs collected in October 2013 (Colonisation Stage 2, CS2, 7 years post-deployment). The distribution of log sizes collected at each stage was approximately the same. In particular, using the definitions of small and large logs given above, 9 large and 7 small logs were collected in CS1, and 10 large and 6 small logs in CS2. In addition, the body size distributions of the assemblages collected at CS1 and CS2 are indistinguishable (linear model, log(body size) ~ CS, $F_{1, 57} = 0.47$, $P = 0.4939$, $R^2 = 0.01$), indicating that changes in the AOR with CS are independent of changes with body size. The two-stage collection process enabled us to test the effect of Colonisation Stage on AORs in two ways. At the community level, we compared AORs calculated across communities collected in CS1 (4760 individuals, 33 species) with those collected in CS2 (8409 individuals, 40 species). At the species level, we compared AORs across species present only in CS1 (n = 8) with those present in both CS1 and CS2 (n = 25), and those present only in CS2 (n = 15).

### *Analysis*

The primary two variables required to fit AORs are *occupancy* and *abundance*. Here, *occupancy* is the proportion of available logs on which a species is present. The number of logs we consider to be available is either the total number of logs sampled (n = 32), the number of logs of a given weight (n = 13 small, 19 large), or the number collected at a given time (n = 16 for both CS1 and CS2). Following established practice in AOR research

(Webb et al. 2012), *abundance* is the mean abundance of a species across available logs on which it is present. We considered two measures of abundance, first using total counts of organisms per log, and second considering density (i.e. individuals per unit mass of log). We prefer the former, and present only these results, because the rarest species on each log is always present as only a single individual, meaning that minimum density scales as 1/mass of log, whereas the abundance of the commonest species on a log is less tightly related to the mass of the log. See Supplementary Materials and figure S2 for details.

We consider proportional occupancy to be the dependent variable in all models, with log(abundance) as one predictor. We log-transform abundance because most species on any one log are rare with a few being extremely common. Because the response variable is proportional, we fit all models as binomial GLMs, using the number of logs over which occupancy is calculated as model weights. To test the predictions set out in table 1 we fit the following models:

Question 1: Is there a relationship between occupancy and abundance across all 48 species and all 32 logs in both collection sets?

Model 1: P(occupancy) ~ log(abundance)

Question 2: Does the interspecific AOR differ between communities with high available energy compared to those with low available energy across all species and both colonisation stages?

Model 2: P(occupancy) ~ log(abundance) * size of log [two-level factor, ‘small’ or ‘large’]

Question 3: Does body size mediate the AOR across all species and all logs in both colonisation stages?

Model 3: P(occupancy) ~ log(abundance) * log(mean body size)

Question 4: Does colonisation stage influence the AOR across all species and logs?

First we consider separately those communities collected after 5yr (CS1) and those collected after 7yr (CS2), and fitted AORs separately for each:

Model 4a: P(occupancy) ~ log(abundance) * community-level CS [two-level factor, '5yr' or '7yr']

Second, we classified species according to which colonisation stage(s) they occurred in (CS1, CS2, or CS1&2) and modelled AORs for each group of species within each CS:

Model 4b: P(occupancy) ~ log(abundance) * species-level CS [four-level factor, CS1 species in CS1, CS2 species in CS2, CS1&2 species in CS1, CS1&2 species in CS2]

We also consider changes between CS1 and CS2 by testing whether species occurring in both (CS1&2) have higher abundances or occupancies within either CS than species occurring in only CS1 or CS2:

Model 5a: P(occupancy) ~ CS ID [two-level factor, CS1 or CS2] * number of CS occupied by species [two-level factor, 1 or 2]

Model 5b: log(abundance) ~ CS ID [two-level factor, CS1 or CS2] * number of CS occupied by species [two-level factor, 1 or 2]

NB Model 5a was fitted as a binomial GLM, model 5b as a Gaussian linear model.

Twenty five species occur in both CS1 and CS2. For these species, we calculate the correlation between change in occupancy and change in abundance between CS1 and CS2. A positive correlation would be consistent with positive intraspecific AORs - i.e. species which declined in abundance over time also declined in occupancy, and vice versa. To further investigate whether these changes were influenced by species-level traits, we fitted the following Gaussian linear model:

Model 6a: Δ(occupancy) ~ Δ(abundance) + initial abundance + initial occupancy + body size + typical log size

Here, Δ(occupancy) and Δ(abundance) are the species-level changes in occupancy and abundance respectively between CS1 and CS2, initial abundance and initial occupancy are abundance and occupancy in CS1, body size is species mean body size, and typical log size is the average mass of logs occupied by a species, weighted by its abundance on each log. This final measure is a way of distinguising between species typically favouring large or small logs (i.e. high or low environmental energy). This model is limited to 21 species occurring in both CS1 and CS2 for which we have body size data. To include all 25 CS1 and CS2 species, we also fitted the model without body size:

Model 6b: Δ(occupancy) ~ Δ(abundance) + initial abundance + initial occupancy + typical log size

All data manipulation and analyses were performed in R 3.2.2 (R Core Team 2015). Data and code are deposited in figshare doi: ##### [available to reviewers on request, public link to be activated on acceptance].

## Results

Across all 48 species and over all 32 logs, there is a strong positive relationship between occupancy and abundance (Model 1: binomial GLM, $b_{log(abundance)}$ = 0.75 (CI: 0.658 - 0.837), z = 16.37, $P < 0.0001$; figure 1A).

There is no evidence that this relationship varies between communities occurring on small logs (low energy availability, 40 species and 13 logs) and large logs (high energy availability, 39 species and 19 logs), with no significant interaction between abundance and size of log (Model 2: $b_{log(abundance)\ x\ size\ of\ log}$ = -0.015 (CI: -0.165 - 0.132), z = 0.20, $P$ = 0.842). Re-fitting this model without the abundance x size of log interaction, there is no evidence that size of log influences the occupancy attained for a given abundance (small logs, intercept = -1.69, CI: -1.93 - -1.45; large logs, intercept = -1.51, CI: -1.75 - -1.29; small-large contrast, z = 0.09, $P = 0.198$). Rather, there is a single relationship between occupancy and log(abundance) very similar to that from the full interspecific model ($b_{log(abundance)}$ = 0.71 (CI: 0.616 - 0.814), z = 14.10, $P < 0.0001$; figure 1B).

Across the 39 species for which we have body size information, the relationship between abundance and occupancy does not vary systematically between large-bodied and small-bodied species (Model 3: no significant interaction between abundance and body size, $b_{log(abundance)\ x\ log(body\ size)}$ = -0.017 (CI: -0.075 - 0.041), z = 0.56, $P = 0.573$). However, re-fitting this model without the abundance x body size interaction reveals that abundance and body size each have significant independent effects on occupancy ($b_{log(abundance)}$ = 0.710 (CI: 0.617 - 0.807), z = 14.63, $P = <0.0001$; $b_{log(body\ size)}$ = 0.078 (CI:-0.010 - 0.148), z = 2.23, $P = 0.0255$). In other words, for a given abundance, larger species tend to have a higher occupancy (especially at low abundances; figure 1C).

The AOR for 16 communities (total 40 species) collected after 7 years (CS2) is significantly steeper than that for 16 communities (total 33 species) collected after 5 years (CS1) (Model 4a: $b_{log(abundance)\ x\ CS}$ = 0.341 (CI: 0.136 - 0.548), z = 3.25, $P = 0.0012$). The value of $b_{log(abundance)}$ in CS1 is 0.53 (CI 0.393-0.670) compared to 0.87 (CI 0.664-1.077) in CS2 (figure 1D).

Considering only those species occurring in both CS1&2, the AOR is steeper in CS2 is steeper than that in CS1 (Model 4b: $b_{log(abundance)}$ in CS1 is 0.37 (CI 0.216-0.529) compared to 0.64 (CI 0.410-0.882) in CS2; CS1 v CS2 contrast = 0.27, z = 2.28, $P = 0.0229$; figure 2A). This is unsurprising given that these species constitute the majority of species in Model 4a above (N = 25 of 33 and of 40 total species in CS1 and CS2 respectively). Coefficient estimates for the 8 species occurring only in CS1 and the 15 species occurring only in CS2 are less precise, and are strongly influenced by a single species in each case (*Xylophaga concava* in CS1, log(abundance) = 2.34, 6.2x higher than any other species occurring in only CS1, Cook's D = 7.34; *Bathyxylophila sp1* in CS2, log(abundance) = 2.97 and p(occupancy) = 0.75, respectively 5.9 and 1.5x higher than any other species occurring only in CS2, Cook's D = 1.06). Excluding these influential species, very little variation in abundance remains across species occurring only in CS1 (6 of 7 remaining species occur at a mean abundance of 1 individual per log), and the coefficient estimate is correspondingly imprecise (2.107, CI -1.076 - 4.886). The coefficient for species occurring only in CS2 is also based on a small range in abundance and is imprecisely estimated, but is significantly steeper than those for species occurring in CS1&2 (1.76, CI 0.912-2.629).

What is clear from figure 2A, however, is that the species attaining highest abundances and occupancies within either CS1 or CS2 are almost all those species that occur in both CS1&2. This is confirmed by Models 5a and 5b (figure 2B, C; table 2): species recorded in only one CS have significantly lower occupancies and abundances *within* that CS than do species recorded in both CS1&2.

Across the 25 species occurring in both CS1 and CS2, there is a strong positive relationship between change in abundance and change in proportional occupancy from CS1 to CS2 (r = 0.64, *P* = 0.0006; figure 3). Fourteen of the 25 species showed correlated changes from CS1 to CS2 consistent with positive intraspecific AORs (11 increased in both abundance and occupancy, 3 decreased in both abundance and occupancy; figure 3). Changes in occupancy were related strongly and positvely to changes in abundance (model 6a, Δ(abundance) coefficient = 0.14, CI = 0.065-0.220). None of the other variables tested was significantly related to changes in occupancy (table 3), but overall the model fit is good ($F_{5, 15}$ = 3.81, P = 0.02, $R^2$ = 0.56). Excluding body size increases the number of species in the model from 21 to 25, but results are similar (model fit: $F_{4, 20}$ = 4.99, P = 0.0060, $R^2$ = 0.50) with Δ(abundance) the only significant predictor (0.14, CI = 0.069-

0.208; table 3). However the coefficient for typical log size approaches significance (0.02, CI = -0.002-0.044; table 3) suggesting a trend for species preferentially occupying larger logs showing more positive changes in occupancy through time.

## Discussion

We have documented significant positive interspecific Abundance-Occupancy Relationships (AORs) in deep-sea, wood-fall communities. Because of the ephemeral nature of wood falls, the communities developing upon them—in particular over the 5-7 year timescale considered here—are bound to constitute primarily species with strong colonisation abilities. Such species are expected to show exactly the kind of saturating positive AOR that we find (figure 1), with no evidence of the critical lower abundance thresholds predicted for species with restricted dispersal (Freckleton et al. 2005). This first demonstration of AORs in deep-sea invertebrates is thus an important extension into the largest habitat on Earth (Dawson 2012) of a macroecological generality concerning the scaling of populations from individual to multiple communities. It also further demonstrates the utility of deep-sea wood-falls as experimental systems in macroecology, offering advantages of both control and tractability (e.g. control of environmental energy, networks of communities established over relatively small spatial and short temporal scales, recovery and complete enumeration of entire communities) and of more observational studies (natural colonisation and establishment of taxonomically diverse assemblages) (McClain et al. 2016). These unique characteristics have enabled us to address a number of questions about the form, strength, and dynamics of AORs, including the role of resource availability (environmental energy), species life histories (body size), and the temporal dynamics of the AOR both within and across species (colonisation stage).

### Environmental Energy

The AOR of communities developing on large (≥4kg) logs was statistically indistinguishable from that of communities developing on small (≤2.5kg) logs (figure 2B), despite the marked difference in environmental energy available to each, and significantly higher biomass and species richness on large logs (McClain et al. 2016, McClain & Barry in review). This lack of a clear difference is not unexpected for two reasons. First, as outlined above, the effect of resource availability on the AOR is likely to be complex. Expressing resource availability as habitat suitability, Freckleton et al. (2006) showed that it is the distribution of suitable habitat (i.e., habitat patches in which species are able to persist) that is critical, rather than the amount per se. Differences in resource availability may also change the extent to which species span both axes of the AOR. For instance, communities with access to more resources may have more equitable species-abundance distributions (Passy 2016), meaning that a smaller range of abundances is represented by the community, potentially reducing power to detect a strong AOR. In addition, the specific deployment of wood falls in this study (see figure S1) meant that large and small logs were interspersed, such that all communities actually developed in a heterogeneous landscape of high and low energy resource. Previous experimental studies have shown that resource heterogeneity has important effects on AORs (Holt et al. 2004), and more generally on colonisation and dispersal dynamics (O'Sullivan et al. 2014), over and above any effects of high and low resource availability. Although individuals developing in resource poor environments may be less able to disperse to neighbouring patches (O'Sullivan et al. 2014), there is no reason to expect the reverse to be the case. To fully test the effects of environmental energy on AORs in this wood-fall system, then, it would be valuable to compare different experimental designs—for instance, deployments of logs of uniformly large or small size, in addition to mixed deployments. Other factors, including wood density and the spacing between logs, could also be manipulated to more closely mimic specific models of habitat distribution such as those considered by Freckleton et al. (2006), and to tease apart the roles of habitat quality *within* patches and dispersal pathways *between* patches.

**Body size**

We show that body size significantly mediated the interspecific AOR of wood-fall communities: for a given mean abundance, larger-bodied species tend to occupy more logs (figure 1C). The body size effect is relatively small (figure 1C depicts relationships for species differing 1000-fold in mass), but indicates that AORs can be influenced by key life history traits. A similar effect of body size has previously been shown for shelf sea macrobenthic infauna, using a much cruder measure of body size (species-level maximum linear dimension, aggregated into categories) (Webb et al. 2009) than we have been able to apply here, suggesting that these patterns are robust to body size measures, even when these measures are applied across invertebrate groups with very different life forms. That study also used maximum density rather than mean density as we use here, making it easy to relate the result to systematic differences in spatial aggregation between small (highly aggregated) and large (less aggregated) species. It is harder to relate mean density directly to spatial aggregation, and in our dataset most species occur on only a small number of logs making robust estimates of species-level aggregation using the distribution of abundances across logs difficult. Nonetheless for the 26 species for which we have a measure of body size and are able to estimate skewness in abundance, all skewness values are positive (indicating right skew, i.e. more logs with low abundance than high abundance), but there is no relationship between skewness and $\log_{10}$(body size) (correlation, $r = -0.08$, df = 24, $P = 0.6834$), where a negative correlation would indicate decreasing aggregation with increasing size. It may be that the small body size effect we observe is indirect, influencing spatial distribution through correlations with, for example, development mode or lifetime reproductive output rather than directly via increased dispersal (Rundle et al. 2009, Webb et al. 2009). Efforts to more directly and robustly quantify the spatial distribution of individuals of different sizes within and between species, at a range of scales, would be useful to further examine this result. In particular, determining how the effect that body size has on the dynamics observed here between a local aggregation of resource patches scales up to effects at wider biogeographical scales would be interesting.

### Colonisation Stage

The AOR is steeper in communities sampled after 7 years (CS2) than in those sampled after 5 years (CS1) (figure 1D). In addition, the range in both abundance and occupancy is somewhat higher in CS2: the only 4 species to occur on all 16 logs within a CS occur in CS2, and the two highest species-level mean abundances are also in this CS, whilst at the same time more species in CS2 are found on a single log (25% cf. 15%) or at a mean density of one individual per occupied log (35% cf. 21%). This is consistent with higher connectedness between communities in CS2, as previously shown in terms of community composition by McClain et al. (2016). A relatively small number of species occurred only in CS1 (n = 8), with almost twice as many unique to CS2 (n = 15), indicating that more time for colonisation allows a greater range of species to reach the wood falls. However, most (n = 25) species occurred in both CS1 and CS2, and these ‘temporal generalist’ species consistently attained higher mean abundances and occupancies *within* either CS1 or CS2 than did the ‘temporal specialist’ species that occurred in only a single CS (figure 2). Moreover, temporal generalists typically occurred on more logs for a given mean abundance than did temporal specialists, especially at low abundances (figure 2A), indicative perhaps of an ability to persist regionally at lower densities as expected for strong dispersers with high colonisation ability (Freckleton et al. 2005).

Considering only those 25 temporal generalist species that were recorded in both CS1 and CS2, a majority (n = 14) demonstrated trajectories in abundance-occupancy space consistent with positive intraspecific AORs - that is, they either increased in both dimensions or decreased in both dimensions (figure 3). This agrees with previous work showing that positive intraspecific AORs are common, but not as ubiquitous as the interspecific relationship (Gaston et al. 2000, Webb et al. 2007, Buckley and Freckleton 2010). It is important to note that communities collected at CS1 were completely harvested, and so these changes reflect wider-scale processes and not simply dispersal between logs collected in CS1 and CS2. There is no significant tendency for combined changes in abundance and occupancy to be greater in species conforming to positive intraspecific AORs (i.e. for arrows in figure 3b to be longer for species occurring in the shaded quadrants of figure 3a; linear model, difference in arrow length between conforming vs non-conforming species = 0.56, CI: -0.254-1.364, t = 1.44, $P = 0.167$), although the four longest arrows are all consistent with positive AORs.

## Conclusions

In conclusion, we have demonstrated that the generally positive relationship between local abundance and site occupancy (the AOR) holds for the diverse assemblages of invertebrates that establish on experimentally deployed deep-sea, wood falls. The features of these wood-fall communities, and details of the experimental design, have enabled us to further examine the roles of environment (energy availability), life history (body size), and time (colonisation stage) in mediating the interspecific AOR; the temporal component has also allowed us to consider intraspecific dynamics. Specifically, we found no effect of environmental energy on the form or strength of the AOR, but our findings did support predictions that larger-bodied species, and communities sampled at a later date (and thus more highly connected) have higher occupancies for a given abundance. In addition, most species recorded at both time points displayed dynamics consistent with positive intraspecific AORs. This general support for positive AORs in the deep sea is important because both the specifics of the experimental wood-fall deployments (e.g. multiple distinct communities developing in close proximity, complete enumeration of entire naturally assembled communities; McClain et al. 2016) and the general properties of the deep sea environment (e.g. low temporal and spatial variation in important environmental variables such as temperature, and the separation of thermal and chemical energy supply; McClain et al. 2012, Webb 2012) make them ideal for testing and further developing mechanistic macroecological theories.

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## References

Bienhold, C. et al. 2013. How Deep-Sea Wood Falls Sustain Chemosynthetic Life. - PLoS ONE 8: e53590.

Blackburn, T. M. et al. 2006. Variations on a theme: sources of heterogeneity in the form of the interspecific relationship between abundance and distribution. - J Anim Ecol 75: 1426–1439.

Borregaard, M. K. and Rahbek, C. 2010. Causality of the relationship between geographic distribution and species abundance. - Q Rev Biol 85: 3–25.

Buckley, H. L. and Freckleton, R. P. 2010. Understanding the role of species dynamics in abundance-occupancy relationships. - Journal of Ecology: 1–14.

Bulafu, C. E. 2015. Disturbance- driven variation in abundance–occupancy relationships over time in tropical forest fragments. - African Journal of Ecology 53: 502–511.

Dawson, M. N. 2012. Species richness, habitable volume, and species densities in freshwater, the sea, and on land. - Frontiers of Biogeography 4: fb_12675.

Fisher, J. A. D. et al. 2010. Dynamic macroecology on ecological time-scales. - Global Ecol Biogeogr 19: 1–15.

Foggo, A. et al. 2007. Do developmental mode and dispersal shape abundance? Occupancy relationships in marine macroinvertebrates? - J Anim Ecol 76: 695–702.

Freckleton, R. P. et al. 2006. Distributions of habitat suitability and the abundance-occupancy relationship. - Am Nat 167: 260–275.

Freckleton, R. P. et al. 2005. Large-scale population dynamics, abundance-occupancy relationships and the scaling from local to regional population size. - J Anim Ecol 74: 353–364.

Gaston, K. J. et al. 2000. Abundance-Occupancy relationships. - J Appl Ecol 37: 39–59.

Holt, A. R. and Gaston, K. J. 2003. Interspecific abundance-occupancy relationships of British mammals and birds: is it possible to explain the residual variation. - Global Ecol Biogeogr 12: 37–46.

Holt, A. R. et al. 2002. The importance of biotic interactions in abundance–occupancy relationships. - J Anim Ecol 71: 846–854.

Holt, A. R. et al. 2004. The importance of habitat heterogeneity, biotic interactions and dispersal in abundance–occupancy relationships. - J Anim Ecol 73: 841–851.

Jenkins, D. G. et al. 2007. Does size matter for dispersal distance? - Global Ecol Biogeogr 16: 415–425.

Lawton, J. H. 1995. Population dynamic principles. - In: Lawton, J. H. and May, R. M. (eds), Extinction Rates. pp. 147–163.

McClain, C. and Barry, J. 2014. Beta-diversity on deep-sea wood falls reflects gradients in energy availability. - Biology Letters 10: 20140129.

McClain, C. R. et al. 2012. Energetics of life on the deep seafloor. - Proceedings of the National Academy of Sciences 109: 15366–15371.

McClain, C. R. et al. 2016. Multiple Processes Generate Productivity- Diversity Relationships in Experimental Wood- Fall Communities. - Ecology 97: 885-898.

O'Sullivan, D. et al. 2014. Inter- patch movement in an experimental system: the effects of life history and the environment. - Oikos 123: 623–629.

Passy, S. I. 2016. Abundance inequality in freshwater communities has an ecological origin. - Am Nat 187: 502–516.

R Core Team 2015. R: A language and environment for statistical computing. - r-project.org.

Rundle, S. D. et al. 2009. By wind, wings or water: body size, dispersal and range size in aquatic invertebrates. - In: Hildrew, A. G. et al. (eds), Body Size: The Structure and Function of Aquatic Ecosystems. Cambridge University Press, pp. 186–209.

Voight, J. R. 2007. Experimental deep-sea deployments reveal diverse Northeast Pacific wood-boring bivalves of Xylophagainae (Myoida: Pholadidae). - J. Mollus. Stud. 73: 377–391.

Webb, T. et al. 2009. Life history mediates large-scale population ecology in marine benthic taxa. - Mar Ecol-Prog Ser 396: 239–306.

Webb, T. J. 2012. Marine and terrestrial ecology: unifying concepts, revealing differences. - Trends Ecol Evol 27: 535–541.

Webb, T. J. et al. 2012. Characterizing abundance-occupancy relationships: there is no artefact. - Global Ecol Biogeogr: 952–957.

Webb, T. J. et al. 2007. Abundance-occupancy dynamics in a human dominated environment: linking interspecific and intraspecific trends in British farmland and woodland birds. - J Anim Ecol 76: 123–134.

Wolff, T. 1979. Magrofaunal utilization of plant remains in the deep sea. - Sarsia 64: 117–143.

**Table Legends**

**Table 1.** Predicted responses of Abundance Occupancy Relationships to increases in proposed mechanistic drivers. In each case, the proposed driver is linked to a variable measured in this study, and the process by which this is linked to the AOR is described. Expected changes in slope and elevation of the AOR are then given.

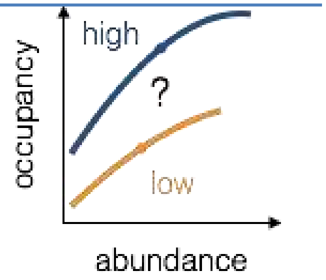
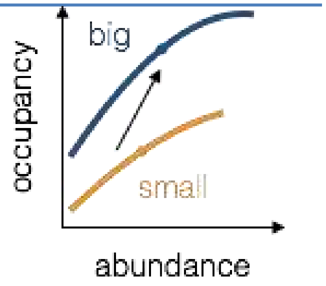
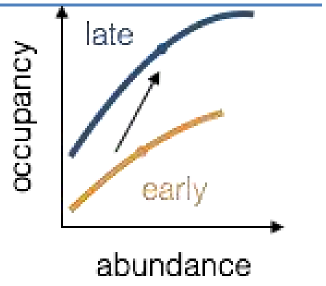
| Mechanistic driver | Measured variable | Process | Predicted AOR response | | |
|---|---|---|---|---|---|
| | | | Slope | Elevation | |
| ↑ Resources | Size of log | More resources support larger local populations, increasing mean local abundance. Larger average local populations mean that more will persist, and that more dispersers will be produced, both of which will tend to increase mean occupancy. This may increase both the slope and elevation of the AOR, but it may also reduce variance in abundance reducing power to detect the AOR. | ? | ?(+) |  |
| ↑ Dispersal | Species mean body size | Larger individuals tend to disperse better as adults, and produce more and larger propagules. All of these mean that patches of suitable habitats will be colonised more rapidly by larger bodied species, strengthening the coupling between local abundance and occupancy, and tending to increase the slope and elevation of the AOR. | + | + |  |
| ↑ Connectivity | Community colonisation stage | More established sets of communities will be composed of more mature populations, and the increased time available for dispersal and colonisation will mean that local populations are more tightly coupled across logs, increasing the slope and elevation of the AOR. | + | + |  |

**Table 2.** Means (with 95% CI) estimated from Models 5a and 5b for proportional occupancy and log(abundance) separately for communities collected after 5 years (CS1) and 7 years (CS2), for species that occur in either CS1 OR CS2, and for species occurring in both CS1 AND CS2.

| | P(Occupancy) | | log(Abundance) | |
|---|---|---|---|---|
| *CS occupied by species:* / *CS sampled* | CS1 OR CS2 | CS1 AND CS2 | CS1 OR CS2 | CS1 AND CS2 |
| CS1 | 0.10 (0.0547-0.162) | 0.46 (0.409-0.506) | 0.36 (-0.551-1.263) | 2.01 (1.493-2.519) |
| CS2 | 0.20 (0.115-0.327) | 0.58 (0.396-0.734) | 0.34 (-0.779-1.467) | 2.05 (0.713-3.388) |

**Table 3.** Models of change in a species' occupancy between CS1 and CS2 as a function of change in its abundance (Δ(abundance)) together with mean body size, abundance in CS1, occupancy in CS1, and the typical size of log occupied by that species. Coefficients and 95% Cis are given, and significant predictors are in bold. Model 6b excludes body size as a predictor, enabling all 25 species to be included (cf 21 in model 6a)

| Predictor | Model 6a | Model 6b |
|---|---|---|
| **Δ(abundance)** | **0.14 (0.065-0.220)** | **0.14 (0.069-0.208)** |
| log(body size) | 0.01 (-0.040-0.064) | / |
| log(abundance in CS1) | 0.003 (-0.080-0.087) | -0.01 (-0.087-0.062) |
| occupancy in CS1 | 0.05 (-0.397-0.497) | 0.10 (-0.318-0.517) |
| typical size of log | 0.02 (-0.006-0.052) | 0.02 (-0.002-0.044) |

## Figure legends

**Figure 1.** Interspecific AORs in deep sea wood fall communities. **A.** Overall AOR for 48 species and 32 logs. Point size is proportional to species mean body size, with open symbols representing species with no body size data. **B.** AORs for 40 species on 13 small logs and 39 species on 19 large logs. **C.** Predicted relationships from Model 3 for species with mean mass 1g and 1000g, showing higher occupancy for a given abundance in larger-bodied species. **D.** AORs for 33 species collected from 16 logs after 5 years (CS1) and for 40 species collected from 16 logs after 7 years (CS2). Occupancy is higher for a given abundance in communities from CS2.

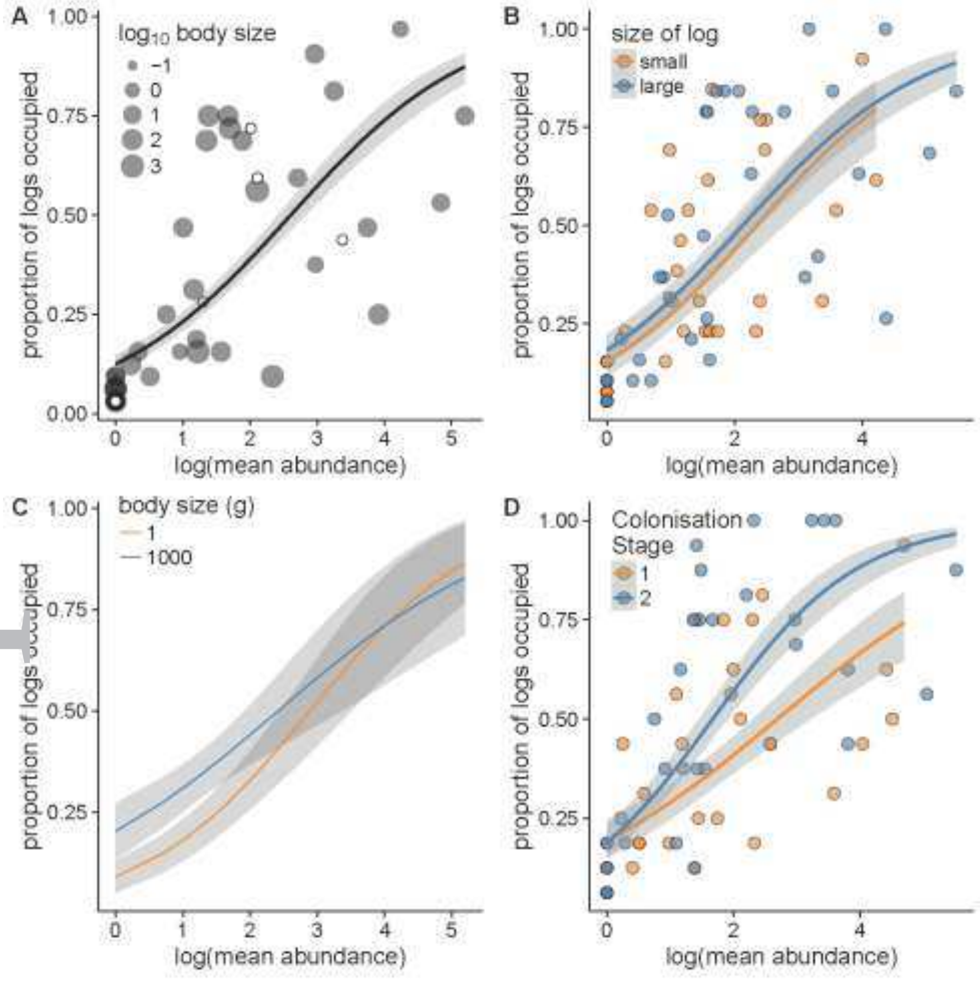


**Figure 2.** Interspecific AORs from deep sea wood fall communities collected after 5 years (CS1) and 7 years (CS1). **A.** Species are classified by the CS they occurred in (CS1, CS2, or CS1&2), and (for those occurring in CS1&2) by the CS sampled (CS1&2_1 and CS1&2_2 show the abundance and occupancy of species occurring in both CS1&2 collected after 5 years and after 7 years respectively). Model fits exclude one highly influential species from both CS1 and CS2 (see text for details). Also shown are boxplots (median, box = IQ range, whiskers = 1.5 x IQ range beyond box) of **B.** log(abundance) and **C.** proportional occupancy for species occurring in CS1, CS1&2, or CS2, collected after either 5 years (CS1) or 7 years (CS2).

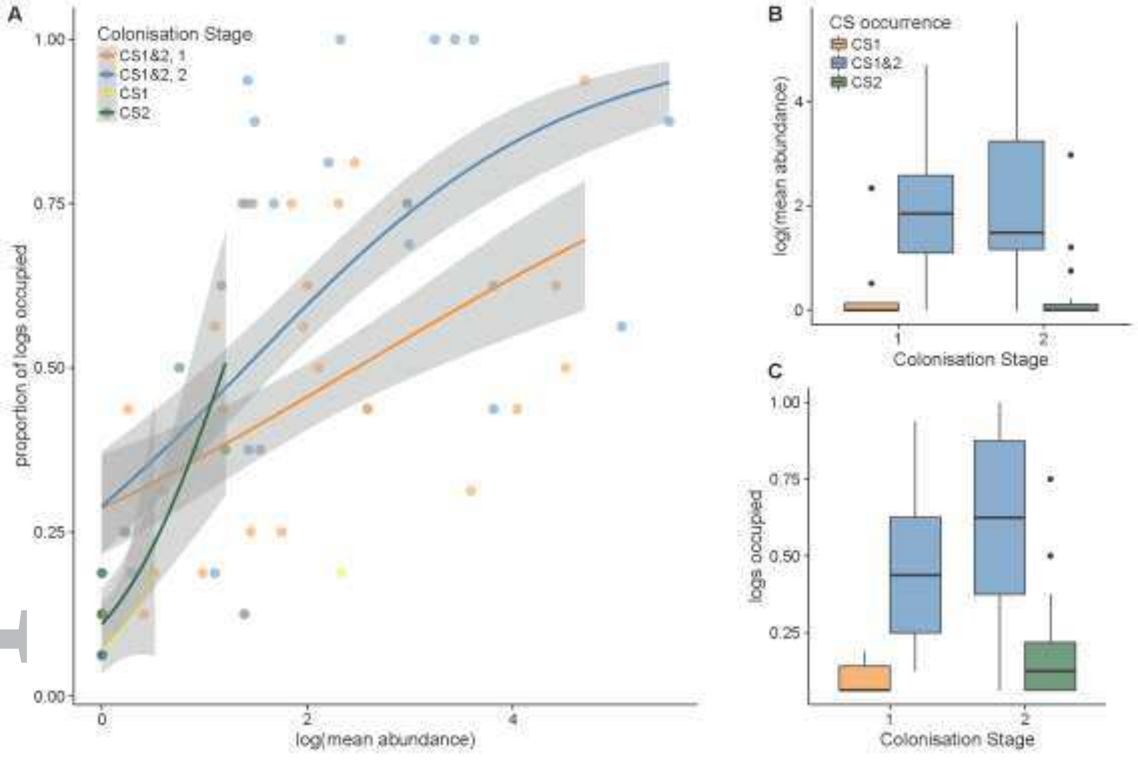


**Figure 3. A.** Changes in mean abundance and proportional occupancy between communities sampled after 5 years and after 7 years for 25 species occurring in both colonisation stages. Orange quadrants indicate correlated changes in abundance and occupancy consistent with positive intraspecific AORs. **B.** Trajectories of the same 25 species illustrated in (A) placed onto the overall interspecific AOR. Arrows start at the position of each species in abundance-occupancy space in communities sampled after 5 years, and arrowheads point to the position of the same species in communities sampled after 7 years.