

1 Deep-sea benthic megafaunal habitat suitability modelling: A global-
2 scale maximum entropy model for xenophyophores

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14
15 **Abstract**

16 The Xenophyophorea is a group of exclusively deep-sea agglutinating rhizarian protozoans, at least
17 some of which are foraminifera. They are an important constituent of the deep-sea megafauna that
18 are sometimes found in sufficient abundance to act as a significant source of habitat structure for
19 meiofaunal and macrofaunal organisms. This study utilised maximum entropy modelling (Maxent)
20 and a high-resolution environmental database to explore the environmental factors controlling the
21 presence of Xenophyophorea and two frequently sampled xenophyophore species that are
22 taxonomically stable: *Syringammina fragilissima* and *Stannophyllum zonarium*. These factors were

23 also used to predict the global distribution of each taxon. Areas of high habitat suitability for
24 xenophyophores were highlighted throughout the world's oceans, including in a large number of
25 areas yet to be sampled, but the Northeast and Southeast Atlantic Ocean, Gulf of Mexico and
26 Caribbean Sea, the Red Sea and deep-water regions of the Malay Archipelago represented
27 particular hotspots. The two species investigated showed more specific habitat requirements when
28 compared to the model encompassing all xenophyophore records, perhaps in part due to the
29 smaller number and relatively more clustered nature of the presence records available for
30 modelling at present. The environmental variables depth, oxygen parameters, nitrate
31 concentration, carbon-chemistry parameters and temperature were of greatest importance in
32 determining xenophyophore distributions, but, somewhat surprisingly, hydrodynamic parameters
33 were consistently shown to have low importance, possibly due to the paucity of well-resolved
34 global hydrodynamic datasets. The results of this study (and others of a similar type) have the
35 potential to guide further sample collection, environmental policy, and spatial planning of marine
36 protected areas and industrial activities that impact the seafloor, particularly those that overlap
37 with these conspicuously large single-celled eukaryotes.

38 Keywords: Maxent; species distribution modelling; Xenophyophorea; *Syringammina fragilissima*;
39 *Stannophyllum zonarium*.

40 1. Introduction

41 Xenophyophores (Schulze, 1904) represent some of the most remarkable megafauna in the deep-
42 sea. These giant rhizarian protozoans build agglutinated tests that, in some cases, reach diameters
43 of over 20 cm (Tendal, 1972; Levin and Thomas, 1988; Gooday *et al.* 2011), and were first
44 described in the late 19th century. Initially they were interpreted as a type of primitive
45 foraminifera (Brady, 1883) or alternatively as a group of horny sponges living in symbiosis with
46 hydroids (Haeckel, 1889). It was not until the early 20th century that xenophyophores were
47 recognised and named as a well defined group at a high taxonomic level within rhizopod protozoans
48 (Schulze, 1904, 1907; Tendal, 1972; Pawlowski *et al.* 2003). Even with this taxonomic recognition,
49 xenophyophores remained in relative obscurity for much of the 20th century, and only after the
50 publication of a landmark monograph in 1972 (Tendal, 1972) did the group become widely known

51 amongst marine biologists in general (Gooday *et al.* 1993; Riemann *et al.* 1993; Pawlowski *et al.*
52 2003; Hughes and Gooday, 2004; Gooday *et al.* 2011).

53 Xenophyophores are a large, conspicuous component of the benthic megafauna found in all major
54 ocean basins (Tendal, 1972; Levin, 1991; Levin and Gooday, 1992; Tendal, 1996) and can be
55 enumerated in deep-water photographs (Kamenskaya *et al.* 2013) due to their often visually
56 distinctive agglutinated tests. These tests enclose a branching system of organic tubes containing
57 the cell body (the granellare system) together with often voluminous masses and strings of waste
58 material (stercomata) enclosed within an organic membrane (Tendal, 1972; Gooday *et al.* 2011).
59 However, observations of living specimens are limited, and so many aspects of xenophyophore
60 biology, reproduction and life cycle remains obscure (Pawlowski *et al.* 2003).

61 Two major xenophyophore lineages are recognised based on morphological criteria: the Psamminida
62 (4 families, 14 genera and over 50 described species), most of which have rigid tests, and the
63 Stannomida (1 family, 2 genera and ~17 described species), which have more flaccid tests, in
64 general, ramified by proteinaceous fibres (linellae) (Tendal, 1972; Tendal, 1996; Gooday and
65 Tendal, 2002; Bisby *et al.* 2010). Opinions about the phylogenetic position of xenophyophores have
66 developed over time. Following initial attempts at classifying xenophyophores (Brady, 1883;
67 Haeckel, 1889) (see above), Schultze (1907) concluded that they represent a distinct group of
68 rhizopod protozoans, an opinion followed by many later workers (Tendal, 1972; Gooday and Tendal,
69 2002). Recently, however, phylogenetic analysis of small sub-unit ribosomal RNA sequences from
70 *Syringamina corbicula* (Richardson, 2001) (Pawlowski *et al.* 2003), *Aschemonella ramuliformis*
71 (Brady, 1884), *Shinkaiya lindsayi* (Lecroq *et al.* 2009) and *Reticulammina cerebiformis* (Gooday *et al.*
72 2011) support Brady's (1883) conclusions that xenophyophores are foraminiferans. However, no
73 sequence data yet exists for stannomids, and so it remains to be proven that all xenophyophores
74 are foraminiferans.

75 Confined to depths greater than about 500 meters, xenophyophores reach peak densities where
76 particle flux to the seafloor is enhanced, such as beneath productive surface waters, in canyons, on
77 areas of raised topography (seamounts or ridges, for instance), or on continental slopes (Tendal,
78 1972; Tendal and Gooday, 1981; Levin *et al.* 1986; Levin and Thomas, 1988; Levin, 1994; Buhl-
79 Mortensen *et al.* 2010; Gooday *et al.* 2011). Xenophyophores may live infaunally in soft mud, but

80 most are epifaunal and live on soft sediment or attached to hard substrates (e.g. Tendal and
81 Gooday, 1981; Gooday *et al.* 2011; Kamenskaya *et al.* 2013). They are likely to feed on a diet
82 comprised mainly of detrital particles that are obtained via suspension feeding, surface-deposit
83 feeding or by being trapped within the complex morphology of the test (Tendal, 1972; Lemche *et al.*
84 *et al.* 1976; Levin and Thomas, 1988; Gooday *et al.* 1993). It has further been suggested that
85 xenophyophores are able to prey on small metazoans (Levin and Gooday, 1992; Smith and
86 Demopoulos, 2003), and may 'farm' microbes as secondary food sources (Tendal, 1979; Laureillard
87 *et al.* 2004; Hori *et al.* 2013), although there is no direct evidence for either of these feeding
88 modes (A. Gooday, personal communication).

89 Xenophyophores sometimes play a significant role in biological processes that occur at the
90 sediment-water interface (Tendal, 1972; Levin and Thomas, 1988; Levin and Gooday, 1992) and
91 large morphologically complex species of genera such as *Reticulammina* (Tendal, 1972) and
92 *Syringammina* (Brady, 1883) can be considered as autogenic ecosystem engineers. For example,
93 xenophyophore tests provide a focus for organic carbon deposition, serving as traps of organic-rich
94 sedimenting particles and add physical heterogeneity to seafloor mineralisation processes (Levin
95 and Thomas, 1988; Levin and Gooday, 1992). Xenophyophore tests represent important habitat-
96 forming structures on the seafloor, contributing significantly to deep-sea biological heterogeneity
97 (Levin and Thomas, 1988; Levin, 1991; Levin and Gooday, 1992; Smith and Demopoulos, 2003; Buhl-
98 Mortensen *et al.* 2010; Hori *et al.* 2013). As a result, large complex tests appear to constitute
99 faunal hotspots in the deep sea (Levin, 1991; Levin, 1994; Hughes and Gooday, 2004), with
100 enhanced faunal densities and species richness (particularly of crustaceans, molluscs, echinoderms,
101 foraminifera and bacteria) in their close vicinity (Levin *et al.* 1986; Hori *et al.* 2013).

102 As such, some xenophyophore species may represent an effective umbrella taxon, and knowledge of
103 their distributions has the potential to be used as a guide, in addition to further information on the
104 distribution of vulnerable marine ecosystems, as to which regions could be designated as marine
105 protected areas (MPAs). Certain areas with abundant xenophyophores may be important for deep-
106 sea biodiversity and so should be considered for protection from human practices that disturb the
107 seafloor, like deep-sea trawling, oil and gas extraction and mining.

108 The great utility of global habitat suitability modelling is in the determination of the potential
109 distributions of taxa that cannot be easily mapped using traditional methods. This is commonly the
110 case in deep-water marine environments, which are difficult to sample due to barriers of cost and
111 isolation. Species distribution models are informative in the context of general scientific
112 investigations (e.g. in targeting regions for further research), but additionally, in cases where the
113 investigated group is of conservation concern (being vulnerable to anthropogenic disturbance
114 and/or important in the functioning of ecosystems) these models can be instructive in directing the
115 designation of protected areas (Davies and Guinotte, 2011; Yesson *et al.* 2012). Maximum entropy
116 modelling (Maxent) (Phillips *et al.* 2006) is a machine-learning habitat suitability modelling method
117 that produces a niche model by minimising the relative entropy between two probability densities;
118 one estimated from the input presence data and the other from the environmental parameters of
119 the landscape in question (Tittensor *et al.* 2010; Elith *et al.* 2011). Maxent has been shown to be
120 one of the highest performing (i.e. most accurate) habitat suitability modelling techniques
121 available (Elith *et al.* 2006; Ortega-Huerta and Peterson, 2008; Wisz, *et al.* 2008). However, its
122 accuracy can drop substantially if a suitable number and variety of presence records are not
123 available to guide the model, and/or if the environmental data available are not reliable or do not
124 fully encompass the range of environmental factors experienced by the focus taxon. There are
125 known issues associated with species distribution models based on small numbers of presence
126 records (Feely and Silman, 2011), including over-prediction, resulting in false positives (Anderson
127 and Gonzalez, 2011), and false negatives. In terms of environmental variables, obtaining a high-
128 resolution global dataset currently requires up-scaling from lower-resolution data, and this
129 inevitably introduces some error, which grows as the difference between native and required
130 resolution increases (Davies and Guinotte, 2011). On balance however, distribution modelling at a
131 global scale remains an instructive and informative technique.

132 This manuscript uses predictive habitat modelling to assess the global probability of occurrence of
133 xenophyophores as a whole taxon and to explore the potential global distribution of the two most
134 commonly recorded xenophyophore species that are also considered taxonomically stable:
135 *Syringamina fragilissima* (Brady, 1883) and *Stannophyllum zonarium* (Haeckel, 1889).
136 Xenophyophore distributions are modelled using a 30 arc-second environmental database, which
137 allows for global modelling at relatively fine spatial scales.

138

139 2. Methods

140 2.1 Xenophyophore presence data

141 A total of 837 independent presence records representing 68 xenophyophore species were obtained
142 from peer-reviewed journals, cruise reports, the Global Biodiversity Information Facility (GBIF) and
143 Ocean Biogeographic Information System (OBIS) (Table 1; Supplementary Table 1). Prior to analysis,
144 this dataset was revised so that only a single record was retained within each 30-arc second cell
145 since multiple presence localities within a single 30-arc second cell can cause habitat suitability
146 values to be weighted in favour of the environmental conditions that exist in that cell (Davies and
147 Guinotte, 2011). As a result, 569 presence records were retained for the distribution modelling of
148 Xenophyophorea, 40 for *Syringammina fragilissima*, and 31 for *Stannophyllum zonarium* (Table 1).

149 Producing a robust species-level distribution model requires a sufficient number of presence
150 records to represent the full observed niche of the species in question as well as confidence in the
151 taxonomic stability and consistency of identification of the chosen species (i.e. that all available
152 records represent a single species, rather than a suite of morphologically similar species).

153 *Aschemonella ramuliformis*, *Aschemonella scabra* (Brady, 1879) and *Reticulammina labyrinthica*
154 (Tendal, 1972) fit this first requirement, with a large number of geo-referenced samples available
155 relative to other xenophyophore species (Table 1). However, there is considerable doubt
156 concerning the taxonomic status of these *Aschemonella* (Brady, 1879) species, and they are
157 probably morphotypes that encompass several similar species rather than representing discrete and
158 consistently identified species (A. Gooday, personal communication). This concern also extends to
159 *Reticulammina labyrinthica*, since it is unlikely that this name has been applied consistently in the
160 literature (A. Gooday, personal communication). As a result, only two species remained for which
161 numerically sufficient taxonomically reliable geo-referenced records were available: *Syringammina*
162 *fragilissima* and *Stannophyllum zonarium*. Hence, only these species were subjected to distribution
163 modelling.

164 2.2 Environmental data

165 In total, 25 environmental layers were produced for use in the Maxent (maximum entropy; Phillips
166 *et al.* 2006) models (Table 2, and see Figure S4 for a correlation matrix of these layers). These
167 were chosen based both on their ecological relevance and their availability at a global scale, and
168 can be split into six broad categories: bathymetric variables (layers derived from a bathymetric
169 grid), carbonate chemistry variables (measures of calcite saturation state), chemical variables
170 (general chemical parameters including salinity, alkalinity and dissolved inorganic carbon amongst
171 others), hydrodynamic variables (current flow), oxygen variables (combination of variables relating
172 to oxygen availability and utilisation), and temperature variables (after Yesson *et al.* 2012).
173 Productivity variables were not available for use owing to a rapid decline in data quality at
174 latitudes greater than ~70°N and S. Since all environmental grids must be of the same latitudinal
175 extent for use in Maxent, and about 22% of xenophyophore presence records were from over 70°N,
176 the decision was made to abandon the use of productivity variables in order to maximise the
177 number of presence records used in the models. However, apparent oxygen utilisation (AOU - the
178 difference in dissolved oxygen concentration of a body of water and its equilibrium oxygen
179 saturation concentration under the same physical and chemical parameters - relating to the use of
180 oxygen due to organismal respiration (Garcia *et al.* 2006a)) was available as a variable, and can be
181 considered a proxy for respiration, which in turn correlates with rates of particulate organic carbon
182 (POC) reaching the benthos (Pfanckuche, 1993).

183 Terrain attributes were extracted from bathymetric data (SRTM30 - a topographical layer produced
184 from a combination of data from the U.S. 'Shuttle Radar Topography Mission' and the U.S.
185 Geological Survey's 'Global 30 Arc-Second Elevation Data Set') following techniques and algorithms
186 described in Wilson *et al.* (2007). Individual approaches are detailed in footnotes within Table 2; a
187 brief description of each variable is given here. Topographic position index (TPI) is an approach to
188 determine topographical features based on their relative position within a neighbourhood, and can
189 be calculated over fine or broad scales to capture smaller or larger terrain features respectively.
190 This calculation has been developed into a GDAL tool (Geospatial Data Abstraction Library) and the
191 approach is described in Wilson *et al.* (2007). Slope was calculated using DEM Tools for ArcGIS
192 developed by Jenness (2012), in particular the 4-cell method of calculating slope, which is
193 accepted as the most accurate approach (Jones, 1998). Here, slope is defined as the gradient in the
194 direction of the maximum slope. Curvature attempts to describe general terrain features and may

195 provide an indication of how water interacts with the terrain. Plan and tangential curvature
196 describe how water converges or diverges as it flows over relief, whilst profile curvature describes
197 how water accelerates or decelerates as it flows over relief (Jenness, 2012). Aspect is defined as
198 the direction of maximum slope and was converted to continuous radians following Wilson *et al.*
199 (2007). Rugosity, terrain ruggedness index and roughness all describe the variability of the relief of
200 the seafloor (Wilson *et al.* 2007). Rugosity is defined as the ratio of the surface area to the planar
201 area across a neighbourhood of a central pixel (Jenness, 2012) while terrain ruggedness index is
202 defined as the mean difference between a central pixel and its surrounding cells and roughness as
203 the largest inter-cell difference of a central pixel and its surrounding cell (Wilson *et al.* 2007).
204 Roughness is calculated as the difference in value between the minimum and maximum bathymetry
205 within a neighborhood (Wilson *et al.* 2007).

206 All other variables were created using the up-scaling approach presented within Davies and
207 Guinotte (2011). All data were available in a gridded form partitioned into standardised depth bins
208 ('z-layers') with a depth range of -0-5500 m. These z-layers facilitated the determination of
209 approximate benthic habitat conditions (of greatest interest owing to the benthic nature of
210 xenophyophores) on a global scale. This was achieved by the projection of each z-layer to its
211 corresponding area of seafloor using the up-scaling approach (Davies and Guinotte, 2011). This
212 process involved three steps: 1) each z-layer was initially interpolated using inverse-distance
213 weighting to a slightly higher spatial resolution (usually 0.1°) in order to minimise potential gaps
214 that could appear between adjacent z-layers due to non-overlap following projection on to the
215 bathymetric layer. 2) These layers were re-sampled to match SRTM30 (Becker *et al.* 2009)
216 resolution (the highest resolution global bathymetric dataset available) and so preserve as high a
217 spatial resolution as possible. 3) Each re-sampled z-layer was draped over the SRTM30 bathymetric
218 layer to provide an indication of conditions near the seabed. Due to the limitations of the global
219 datasets currently available, it had to be assumed that conditions below the deepest z-layer
220 available were stable to the seabed. However, this approach has been demonstrated to work well
221 over global and regional scales (Davies and Guinotte, 2011; Guinotte and Davies, 2012).

222 Since the incorporation of too many variables into a habitat suitability model can cause over-fitting
223 of the model (Beaumont *et al.* 2005), a small subset of the available environmental layers were

224 selected for use in the final analyses. Owing to the co-variant nature of many of the layers in each
225 of the six variable categories (Figure S4), a single variable from each category was selected to
226 represent the influence of that category (following the method of Yesson *et al.* 2012). Variable
227 selection for each category was based on the predictive power of models based on single
228 environmental layers. This was measured using the Test AUC statistic (area under the receiver
229 operating characteristic - ROC - curve; Fielding and Bell, 1997). The AUC statistic can be defined as
230 the probability that a presence site is ranked above a random background site. Values vary from 0
231 (model performance worse than random) to 0.5 (model performance indistinguishable from
232 random) to 1 (model is maximally predictive) (Fielding and Bell, 1997). Test AUC is quoted since it
233 is more reliable than training AUC scores (Warren and Seifert, 2011). Thus the single variable that
234 produced the greatest test AUC value in isolation for each biological category was selected to
235 represent that category in the final analyses, and hence the final analyses utilised six
236 environmental layers (Table 3 and Table 4).

237 2.3 Maximum entropy predictions

238 Maxent (Phillips *et al.* 2006) version 3.3.3k was used to perform the global distribution prediction
239 analyses. Default model parameters were used (convergence threshold of 10^{-5} , regularisation
240 parameter of 1 and a maximum iterations value of 500, with 10000 points randomly selected as
241 background data to construct the model and each model run setting aside 30% of presence records
242 for model evaluation) since these settings have been shown to produce reliable results (Phillips and
243 Dudik, 2008; Davies and Guinotte, 2011; Yesson *et al.* 2012). Higher regularisation parameter values
244 were trialled for the more taxonomically inclusive model of Xenophyophorea to produce smoother
245 response curves (Figure 2). However, this resulted in the production of over-generalised models,
246 lower test AUC, increased differences between training and test AUC, and a less discriminatory
247 model output.

248 Model performance was evaluated by considering entropy, test AUC, test gain, and test omission
249 scores (see Phillips *et al.* 2006). The importance of each environmental variable was assessed using
250 a jack-knifing procedure (by comparing the gain achieved by variables in isolation - jack-knife of
251 regularised training gain). Response curves were produced to visualise how xenophyophore habitat
252 suitability varied with each environmental factor analysed.

253

254 3. Results

255 3.1 Sample locations

256 Xenophyophore sampling to date is patchily distributed throughout the world's oceans (Figure 1).
257 Areas where the highest numbers of xenophyophores have been collected include the North Atlantic
258 (the Porcupine Abyssal Plain, Rockall Bank, Monaco Basin, Cape Verde Plateau and along the Mid-
259 Atlantic Ridge), the Gulf of Mexico, the South Atlantic (especially around the Rio Grande Rise and
260 Mid-Atlantic, Atlantic-Indian and Walvis Ridges) and Atlantic portion of the Southern Ocean, the
261 Arctic Ocean (Baffin Basin, Barents Sea, Nansen Basin, Amundsen Basin and Makarov Basin in
262 particular), patchily in the Indian Ocean (Somali Basin and off the coast of South Africa in
263 particular) the South China Sea, the Northwest Pacific Basin, the Peru Basin, and around New
264 Zealand. In contrast, xenophyophores have been only sparsely collected from the majority of the
265 Indian and Southern Oceans, the western Arctic Ocean, and the South Pacific Ocean.

266 The global distribution of xenophyophore samples (Figure 1) cannot be directly interpreted in terms
267 of overall sampling effort, but the patterns described above suggest that deep-water investigations
268 are concentrated close to nations with more established sampling programmes, as well as hinting of
269 potential bias against more remote locations (the Southern Ocean, for instance).

270 3.2 Variable selection

271 Test AUC scores for the models based on a single variable varied greatly - from a minimum value of
272 0.393 (topographic position index, *Syringammina fragilissima*) to a maximum of 0.987 (depth,
273 *Syringammina fragilissima*) (Table 3). Considering the six variable groupings (Table 2), depth
274 performed best of all bathymetric variables across the taxa, whilst the curvature variables and
275 topographic position index consistently produced some of the lowest AUC scores. Calcite saturation
276 state returned high AUC scores for all taxa analysed, as did all chemical variables analysed (with
277 nitrate, phosphate and silicate in particular performing consistently well), oxygen variables (with
278 apparent oxygen utilisation, in particular, scoring highly) and temperature. AUC values for
279 hydrodynamic variables were generally low, but regional flow rate consistently outperformed

280 vertical flow rate (Table 3). The highest scoring variables in each variable group for each taxon
281 were chosen for use in the multivariate Maxent models (see Table 3 and Table 4).

282 3.3 Multivariate model evaluation

283 Test AUC scores for the multivariate Maxent models were high (Table 4), ranging from 0.836
284 (Xenophyophorea) to 0.997 (*Syringammia fragilissima*). Test gain values ranged from 0.841
285 (Xenophyophorea) to 4.580 (*Syringammia fragilissima*), while entropy values ranged from 8.632
286 (Xenophyophorea) to 4.512 (*Syringammia fragilissima*). Test omission scores were low, ranging
287 from 0.200 (Xenophyophorea) to 0.000 (*Syringammia fragilissima* and *Stannophyllum zonarium*)
288 (based on the maximum sensitivity plus specificity of the test dataset). These low omission scores
289 indicate that few known presences were wrongly classified as absences by the models, and that the
290 predicted presences were significantly more probable than that of random background pixels (Table
291 4).

292 3.4 Taxa niches

293 Jack-knife assessment of model regularised training gain was used to determine which three
294 variables were most important in the production of each of the multivariate Maxent models (Table
295 4). Combining this with information present in Figure 2, the main environmental conditions for peak
296 habitat suitability (defined as a logistic habitat suitability of ≥ 0.5) - i.e. the niche - for each taxon
297 were estimated. For *Syringammia fragilissima* these were a depth of between -835 and 1180 m, a
298 calcite saturation state of between -2.56 and 3.36, and a temperature of between -5.3 and 7.7 °C.
299 For *Stannophyllum zonarium*, these were a nitrate concentration greater than 37.5 $\mu\text{mol l}^{-1}$,
300 apparent oxygen utilisation values of between 4.50 and 6.32 $\text{mol O}_2 \text{m}^{-3}$, and temperatures of
301 between 1.6 and 4.7 °C.

302 It is more complex to estimate conditions of peak habitat suitability for Xenophyophorea since the
303 model encompasses the varied habitat requirements of multiple species (including those described
304 above) and hence produced variable responses that had multiple peaks (Figure 2). Considering this,
305 high habitat suitability for the taxon occurred at nitrate concentrations of -12.5 to 29.2 $\mu\text{mol l}^{-1}$
306 and above 38.0 $\mu\text{mol l}^{-1}$, oxygen saturations of between 6.6 and 42.6 % O_2^s , between 69.2 and 74.3

307 %O₂^S and between 82.1 and 89.7 %O₂^S, and temperatures ranging from ~-0.8 to -0.6 °C and ~-2.4 to
308 8.7 °C.

309 For Xenophyophorea and *Syringammina fragilissima*, temperature was the variable that both
310 reduced the training gain by the greatest amount when omitted from the multivariate Maxent
311 model and produced the highest gain when used in isolation. Hence, this variable contained the
312 most useful information that was not present in the other variables used to construct the models
313 and the most useful information when used in isolation (Table 4). For *Stannophyllum zonarium*,
314 apparent oxygen utilisation contained the most information that was not present in the other
315 variables and the most useful information when used in isolation (Table 4).

316 At the other end of the spectrum, regional flow rate consistently contributed very little to the
317 Maxent multivariate models, whilst depth and calcite saturation state contributed relatively little
318 to the niche model of *Stannophyllum zonarium* (Table 4).

319 3.5 Areas of maximal habitat suitability

320 For Xenophyophorea (see Figure 3 and Figure S1), areas of peak habitat suitability were centred on
321 a range of bathymetric features, including continental slopes, subduction trenches, semi-enclosed
322 seas, ridges, seamounts and plateaus. In the Atlantic, xenophyophore habitat suitability was high
323 along all continental slopes, around the Rio Grande Rise, along the Walvis, Reykjanes and Mid-
324 Atlantic Ridges, in the Gulf of Guinea, on the Cape Verde Plateau and plain, in the Angola,
325 Porcupine and Biscay abyssal plains, the most westerly extent of the Mediterranean Sea, around
326 Rockall Bank and the Icelandic Plateau, along the Davies Strait and in Baffin Bay, around the
327 Flemish Cap, in the Gulf of Mexico, and in deep water areas off Florida and in the Caribbean Sea.
328 Habitat suitability was essentially zero on all continental shelves, in all but the very western extent
329 of the Mediterranean and Sargasso seas, on the Sohm and Hatteras Plains, and in the, Sierra Leone,
330 Guinea, Brazil, Argentine and Cape Verde Basins.

331 Habitat suitability was moderate in the Arctic Ocean (between 0.3 - 0.8 logistic suitability), and
332 hotspots were centred upon the continental slopes, Voring Plateau, Greenland Sea, Denmark Strait,
333 Baffin Bay, and Lomonosov Ridge (Figure 3).

334 The Southern and Indian oceans exhibited only isolated areas of high habitat suitability for
335 xenophyophores, relative to the Atlantic Ocean. These included points along continental slopes
336 (save for the Antarctic continental slope), the South Tasman Rise and the Exmouth Plateau, along
337 Broken Ridge, scattered points along Ninetyeast Ridge, parts of the Agulhas, Madagascar and
338 Mozambique plateaus, regions of the Carlsberg ridge, along the Chagos-Laccadive ridge, the
339 Mascarene Plateau, and regions of high suitability in the north of the Bay of Bengal, the
340 Lakshadweep Sea, Gulf of Aden and deepest parts of the Red Sea. Further south, the South
341 Sandwich Trench is also notable for relatively high habitat suitability (Figure 3).

342 The Malay Archipelago exhibited very high habitat suitability for xenophyophores in general.
343 Particularly suitable areas included the Andaman Sea (particularly Dreadnought Bank) and the
344 South China Sea, Sulu Sea, Celebes Sea and Banda Sea. In the southwest Pacific, the Bismarck Sea,
345 Ontong Java Rise and regions of the Coral Sea showed areas of relatively high habitat suitability.
346 Regions of suitable habitat were also found around New Zealand - particularly on the Challenger
347 Plateau and Chatham Rise, and along the Kermadec and Tonga trenches and associated ridges
348 (Figure 3).

349 In the Pacific proper, high habitat suitability was generally centred along subduction trenches,
350 continental slopes and numerous seamounts. For example, along the Mariana, Ryukyu, Izu-
351 Ogasawara, Japan and Kuril-Kamchatka trenches and associated ridges to the west, the Mid-Pacific
352 Mountains, Emperor Seamount chain, and around the Hawaiian ridge and Islands. High habitat
353 suitability was also highlighted along the Cocos and Carnegie Ridges, along the length of the Peru-
354 Chile Trench, in the deep water off the Californian coast, the northern-most extent of the Bering
355 Sea, in the deeper regions of the Sea of Okhotsk and to the west of the Ryukyu Islands (Figure 3).

356 The model for *Syringamina fragilissima* produced the smallest area of suitable habitat of the taxa
357 investigated (Table 4, Figure 4, Figure S2), being restricted to around Rockall Bank, the Hebrides
358 Terrace and Anton Dohrn Seamounts, Rosemary Bank, along the Wyville Thomson Ridge, points on
359 the continental slope along the west of the United Kingdom, the Iceland-Faeroe Rise, the
360 continental slope around Iceland and the Reykjanes Ridge, along the Mid-Atlantic Ridge close to the
361 Azores, around the northernmost extent of the Labrador Sea, north of the Bahamas, along the
362 shallowest regions of the Madagascar Plateau, and points around New Zealand (particularly in areas

363 of the Campbell Plateau). However, it must be stressed that, due to the limited number of
364 presence records available for this species, and their relatively clustered nature (and so the
365 requirement of extrapolation over relatively large areas in the model - such as over the South
366 Atlantic, North and East Pacific, Arctic Ocean and Indian Ocean), the above does not represent a
367 definitive map of distribution for the species. The addition of further presence records (particularly
368 in regions yet to be sampled) may alter the area of apparent high habitat suitability for
369 *Syringamina fragilissima*.

370 The model for *Stannophyllum zonarium* (Figure 5 and Figure S3) highlights a broader distribution
371 than for *Syringamina fragilissima*, with areas of maximal habitat suitability centred on the Pacific
372 Ocean rather than the Atlantic Ocean. Areas of high habitat suitability include much of the East and
373 Northeast Pacific (Guatemala Basin and Albatross Plateau in particular), along the northern slope of
374 the Aleutian Trench, around the Hawaiian Islands and Ridge, the Mid-Pacific Mountains, along
375 Sculpin Ridge, in the Aleutian Basin (particularly the northernmost extent), along the Emperor
376 Seamount Chain, on the Hess and Shatsky rises, in the Kuril Basin, along the Mariana, Ryukyu, Izu-
377 Ogasawara, Japan and Kuril-Kamchatka trenches and associated ridges to the west, to the South of
378 Japan, the Ontong Java Rise, Caroline Seamounts, and isolated areas in the Coral Sea. In the Malay
379 Archipelago, areas of high habitat suitability include deep areas of the Andaman, Sulu and South
380 China seas, the Celebes Sea, the Makassar Strait and North Banda Basin, and areas of the Molucca
381 and Flores Sea. In the Indian Ocean, the northernmost extent of the Bay of Bengal, regions of the
382 Arabian Sea and Gulf of Aden, points along the Mascarene and Chagos-Laccadive plateaus and areas
383 of continental slope along the northern shores of the ocean show high habitat suitability for this
384 species (Figure 5). However, as for *Syringamina fragilissima* above, this distribution should not be
385 interpreted as definitive due to the relatively small number of presence records available (and the
386 requirement of extrapolation in the model such as over the Indian, Atlantic and polar oceans). The
387 addition of further presence records may alter the area of apparent high habitat suitability for
388 *Stannophyllum zonarium*.

389 4. Discussion

390 4.1 Habitat predictions and applications

391 This exploratory study enhances both our knowledge of xenophyophore distributions and illuminates
392 the controlling physical factors of these distributions. It is generally accepted that xenophyophores
393 reach highest densities in regions of high surface productivity (Tendal, 1972), and in areas where
394 the flux of organic particles is enhanced by topography (Levin and Thomas, 1988; Levin, 1994;
395 Gooday *et al.* 2011), including seamounts, mid-ocean ridges, canyons, subduction trenches,
396 plateaus and continental slopes (Lemche *et al.* 1976; Tendal and Lewis, 1978; Levin and Thomas,
397 1988; Levin, 1994; Gooday *et al.* 2011). These topographic features are associated with localised
398 currents (e.g. Roden, 1987), and thus it is hypothesised that organic particles are concentrated in
399 their vicinity, increasing food availability for xenophyophores. As an alternative, Levin and Thomas
400 (1988) suggest that the localised current regimes around these topographic features result in an
401 increased flux and/or deposition of xenophyophore propagules. Whilst productivity or localised
402 current flow data were not available for use in this analysis (although apparent oxygen utilisation
403 can be thought of as a proxy for productivity, and terrain variables can capture topographical
404 driven flow information), predicted xenophyophore distributions (Figures 3, 4 and 5) were broadly
405 concordant with the accepted views above. High habitat suitability scores were commonly obtained
406 for mid-ocean ridges, continental slopes, plateaus, seamounts and the slopes of subduction
407 trenches. This suggests that these topographic features may be associated with additional
408 environmental characteristics positive to xenophyophore growth. Interestingly, in addition to the
409 topographic features outlined above, this analysis suggests that deep semi-enclosed seas and bays
410 may also be favourable to xenophyophore growth. For example, Baffin Bay, the Gulf of Mexico, the
411 Caribbean Sea, the South China Sea, Andaman Sea, Sulu Sea, Celebes Sea and Banda Sea all exhibit
412 high habitat suitability (Figure 3), although the Mediterranean Sea is an exception to this.

413 Comparison of the global sampling distribution (Figure 1) and the habitat suitability map for
414 xenophyophores (Figure 3) reveals that some xenophyophores have been sampled from areas with
415 relatively low predicted habitat suitability. These include the Mediterranean Sea, the Southern
416 Ocean and along the coast of Antarctica, around the southernmost extent of the Brazil Basin and
417 northernmost extent of the Argentine Basin, to the southeast of Sri Lanka, to the north of
418 Madagascar and parts of the Northwest Pacific and Arctic Ocean. Incorrect identification or spatial
419 referencing errors may explain some of these records. Alternatively, the xenophyophore
420 distribution model may not fully reflect the potential distribution of the group, or these samples

421 may represent collection of xenophyophores in fringe habitats where they naturally occur at low
422 densities.

423 When xenophyophore sampling locations (Figure 1) are compared with the Maxent habitat
424 suitability maps (Figures 3, 4 and 5) it is demonstrated that a significant number of locations with
425 high predicted xenophyophore habitat suitability are yet to be sampled. For Xenophyophorea, these
426 include much of the western Arctic Ocean, the Icelandic Plateau and Reykjanes Ridge, most of
427 Baffin Bay and the Labrador Sea, around the Flemish Cap, much of the Caribbean Sea, the Angola
428 Basin, many locations along the continental slopes of the East and West Atlantic, most of the Mid-
429 Atlantic Ridge, the Madagascar and Mascarene plateaus, the Gulf of Aden, the north of the Bay of
430 Bengal and much of the Indian Ocean continental slopes of Australia, the Andaman Sea and seas
431 around Sulawesi in the Malay Archipelago, around the Ryukyu Islands, the Ontong Java Rise, the
432 northernmost extent of the Bearing Sea, much of the Sea of Okhotsk, and numerous seamounts in
433 the Pacific Ocean which are yet to be investigated. For *Syringammina fragilissima*, such areas are
434 less numerous, but include the Reykjanes Ridge and the Mid-Atlantic Ridge around the Azores, the
435 northernmost extent of the Labrador Sea, and potentially to the north of the Bahamas and on
436 Walters Shoal of the Madagascar Plateau. For *Stannophyllum zonarium*, such areas are numerous
437 and include much of the East and Northeast Pacific, along the Hawaiian and Boudeuse ridges, the
438 deepest parts of the Bering Sea (particularly the northern slopes of the Aleutian Basin), along the
439 Emperor Seamount Chain, along the major trenches of the West Pacific, on the Ontong Java Rise,
440 the Andaman, South China, Sulu, Celebes and Banda Seas, the north of the Bay of Bengal, and the
441 Arabian Sea. These locations represent key targets for future sampling.

442 In regions where there is a perceived threat to benthic environments, the presence of a high
443 density of large, morphologically complex xenophyophore species, in conjunction with other
444 vulnerable marine ecosystems, could be considered as further motivation for the instalment of
445 deep-water MPAs, since many xenophyophore species are important but fragile autogenic
446 ecosystem engineers, playing a significant role in biological processes that occur at the sediment-
447 water interface (Tendal, 1972; Levin and Thomas, 1988; Levin, 1991; Levin and Gooday, 1992;
448 Smith and Demopoulos, 2003; Hughes and Gooday, 2004; Hori *et al.* 2013). For instance, this
449 analysis provides possible direction for the instalment of MPAs in areas of high predicted

450 xenophyophore habitat suitability that are currently subjected to deep-sea bottom trawling. Such
451 areas include a large number of seamounts, banks, ridges and plateaus across the world's oceans
452 (Figure 3) (e.g. see Koslow *et al.* 2000 and Thrush and Dayton, 2002), and, indeed, some such areas
453 have already been protected based on evidence of the presence of vulnerable marine ecosystems
454 (including xenophyophore aggregations) (e.g. the Darwin Mounds off the NW coast of Scotland (De
455 Santo and Jones, 2007)). This analysis also potentially provides spatial guidance for the protection
456 of areas vulnerable to local negative ecosystem impacts associated with deep-sea oil and gas
457 drilling, such as around the 'Atlantic Frontier' drilling sites near the Faroe Islands and sites in the
458 Gulf of Mexico (Glover and Smith, 2003) (Figure 3). Similar knowledge and data could be applied to
459 help propose MPAs in areas earmarked for deep-sea mining operations, such as areas of the Manus
460 Basin off New Guinea and the Havre Trough off New Zealand (Glover and Smith, 2003), and the
461 Clarion-Clipperton Fracture zone in the Eastern Pacific (where xenophyophores are known to reach
462 quite high abundances) (Kamenskaya *et al.* 2013) (Figures 3 and 5). However it should be stressed
463 that, although the resolution of this analysis is very high for its global scale, it is not adequate for
464 probing the fine-scale distributions of xenophyophores within areas of high apparent habitat
465 suitability, and as such, targeted surveys and distribution modelling of potential MPA locations at
466 local or regional scales should be undertaken before designation to ensure they are based on the
467 highest quality observational data available (Rengstorf *et al.* 2012; Ross and Howell, 2012; Guinotte
468 and Davies, 2012; Rengstorf *et al.* 2013).

469 4.2 Taxa niches

470 Depth was one of the most important variables defining habitat suitability for the taxa analysed
471 (Table 4). Moving from sea-level to greater depths, habitat suitability increased to values over 0.5
472 only in depths greater than about 500 m (Figure 2). This agrees well with the accepted observation
473 that xenophyophores are found in water depths greater than ~500 m (Tendal, 1972; Levin, 1994;
474 Buhl-Mortensen *et al.* 2010). The importance of depth was not unexpected since multiple factors of
475 biological importance also change with depth, including light intensity, pressure, temperature,
476 productivity, salinity, calcium carbonate saturation states, and many more chemical variables. The
477 trough in xenophyophore habitat suitability between about 4800 and 6350m depth was unexpected,
478 however (Figure 2). It is possible that this is caused by unfavourable environmental conditions for

479 xenophyophores at these depths, such as nutrient-depletion. Alternatively this trough could reflect
480 the lack of environmental data available at depths of >5500 m from many global data products (i.e.
481 World Ocean Atlas). What is most likely, however, is that this habitat suitability trough represents
482 an artefact of poor sampling effort at these depths.

483 Nitrate concentration was found to be an important environmental parameter for Xenophyophorea
484 as a whole and for *Stannophyllum zonarium*. Peak xenophyophore habitat suitability was found to
485 occur in waters with relatively high nitrate concentrations, and at particularly high nitrate
486 concentrations for *Stannophyllum zonarium* in particular (maximal habitat suitability at
487 concentrations greater than 37.5 $\mu\text{mol l}^{-1}$) (Figure 2). This finding agrees well with the notion of
488 xenophyophores being most common in relatively nutrient-enriched waters (Tendal, 1972; Levin
489 and Thomas, 1988; Levin, 1994; Gooday *et al.* 2011).

490 The importance of calcite saturation state as a habitat characteristic relevant to xenophyophore
491 distributions (Table 4) has, to the authors' knowledge, never been explicitly stated, although it has
492 been observed that xenophyophores exhibit a 'preference' for sand-sized particles in test
493 construction (Levin and Thomas, 1988; Levin, 1994), and that foraminiferal tests are a common
494 sand-sized component in many xenophyophore tests (A. Gooday, personal communication). It seems
495 that for multiple (but certainly not all) xenophyophore species, a calcite saturation state >1 is
496 associated with test production from recycled calcareous foraminifera. This would appear to be the
497 case for *Syringammina fragilissima*, for instance, with this commonly foraminiferal-tested (Tendal,
498 1972) species occurring well above the carbonate compensation depth and experiencing peak
499 habitat suitability in waters with a calcite saturation state of between ~2.56 and 3.36 (Figure 2).

500 Oxygen variables were important in model construction for Xenophyophorea and for *Stannophyllum*
501 *zonarium* in this study. Per cent oxygen saturation was an important variable for Xenophyophorea
502 (Table 4), with the taxon exhibiting peaks of habitat suitability at a range of saturations - from 6.6
503 up to 89.7 %O₂^S (Figure 2). Such a broad range of suitable oxygen saturations demonstrates a high
504 level of variability in oxygen requirements and tolerance amongst species in this taxon, although
505 most xenophyophores have been sampled from relatively well-oxygenated regions (A. Gooday,
506 personal communication). Apparent oxygen utilisation was the most important variable in the
507 construction of the Maxent model for *Stannophyllum zonarium*. Interestingly, this species reaches

508 peak densities at apparent oxygen utilisation values of between 4.50 and 6.32 mol O₂m⁻³ (Figure 2).
509 Such high values link well with the high nitrate concentration preferences of *Stannophyllum*
510 *zonarium*, suggesting that this species is often sampled from productive nutrient enriched regions
511 with particularly high associated biological activity.

512 Temperature was of consistent importance to all taxa investigated, and was the single most
513 important variable in the construction of the Maxent models of Xenophyophorea and *Syringammina*
514 *fragilissima* (Table 4). The two species investigated in detail exhibited discrete temperature
515 windows of peak habitat suitability (between -5.3 and 7.7 °C for *Syringammina fragilissima*,
516 compared to between -1.6 and 4.7 °C for *Stannophyllum zonarium*) (Figure 2). The relationship
517 between xenophyophore occurrence and temperature has not been discussed in detail, although
518 there is some mention by Tendal (1972). Here Tendal argues that, as xenophyophores are to be
519 considered members of a distinct cold-water fauna, it is to be expected that they are restricted in
520 their upper vertical distributions by increasing temperature with decreasing depth, although he
521 does not expand as to why this should be. More generally, such relationships are well documented
522 for marine invertebrates (e.g. see Orton, 1920 and Barras *et al.* 2009), with temperature being an
523 important factor controlling growth rate and various aspects of reproductive physiology, mediated
524 by its influence on biochemical reactions (Brown *et al.* 2004).

525 Finally, it is interesting to note the low AUC values (Table 3) and low jack-knife training gains
526 (Table 4) that were obtained for the hydrodynamic variables for all taxa investigated (regional flow
527 for *Syringammina fragilissima* being a potential exception). This was surprising since the
528 importance of water flow for xenophyophores as suspension feeders has been stressed by many
529 authors (Tendal, 1972; Tendal and Lewis, 1978; Levin and Thomas, 1988; Levin, 1994). However,
530 hydrodynamic variables also performed badly in a recent study of cold-water coral distributions
531 (known suspension feeders) (Yesson *et al.* 2012) which used a similar environmental dataset. Thus
532 this poor performance is likely to represent a scale issue - with these global scale layers not
533 accurately portraying local scale variations in current velocity associated with small topographic
534 features (Yesson *et al.* 2012). Higher resolution data is required to shed further light on the
535 importance of current flow for the distribution of megafaunal suspension-feeders (Mohn *et al.*
536 2014).

537 4.3 Model evaluation and limitations

538 Model performance was good for all taxa, with high test AUC and gain scores, and low test omission
539 values. Test AUC and gain values were higher for the species investigated compared to
540 xenophyophores as a whole, and were higher for *Syringammina fragilissima* than for *Stannophyllum*
541 *zonarium*. This was probably a result of the greater level of clustering of *Syringammina fragilissima*
542 sample locations relative to *Stannophyllum zonarium*. The models for *Syringammina fragilissima*
543 and *Stannophyllum zonarium* had a less variable dataset to fit than for Xenophyophorea, with
544 smaller total variance in the environmental parameters at their sampling localities (smaller entropy
545 values - see Table 4) as a result of the smaller number of presence records used in the models.
546 Thus the Maxent model could be fitted more tightly around the presence data.

547 There are known issues associated with species distribution models produced using small numbers
548 of presence records (Feely and Silman, 2011), these chiefly being over-prediction, resulting in false
549 positives (Anderson and Gonzalez, 2011), and false negatives. The use of presence records that are
550 distributed across a large longitudinal and latitudinal range (as for the model for Xenophyophorea)
551 should lower the risk of over-prediction, and in general, the models appear to have performed well.
552 However, there is some evidence of small areas of false positives. For example, in Figure 3
553 (Xenophyophorea), relatively shallow areas (<500 m depth) of the Norwegian trough are highlighted
554 as potentially suitable habitat (0.4-0.6 logistic habitat suitability), while in Figure 5 (*Stannophyllum*
555 *zonarium*), small areas of the Shelikof Strait are highlighted as suitable habitat (0.7-0.9 logistic
556 habitat suitability) in water depths of around 200m. Considering our current knowledge of
557 xenophyophore bathymetric distributions (see above and Figure 2), these predictions almost
558 certainly represent false positives, although only ground-truthing can confirm this. False negatives
559 are harder to pinpoint in the Maxent predictions, but almost certainly occur to some extent in the
560 models for *S. fragilissima* and *S. zonarium* presented here (considering the level of extrapolation
561 across ocean basins from a relatively small number of presence records). The addition of further
562 presence records (particularly in regions yet to be sampled) will help to better define the
563 distributions of these two species and highlight any false negatives present in the current models.

564 Comparison of the habitat suitability predictions obtained in the present study with those of the
565 only other Maxent model yet produced for a xenophyophore species (Ross and Howell, 2012)

566 represents a further way in which model performance can be evaluated. In general, the two models
567 show a high level of similarity. High habitat suitability (>0.6) for *Syringammina fragilissima* in the
568 NE Atlantic is demonstrated in both models along the continental slope off Ireland and the United
569 Kingdom, around the Hebrides Terrace and Anton Dohrn seamounts, around Rosemary Bank, and
570 along the slopes of Rockall and Hatton banks. There are some areas where the two models
571 disagree, however. For instance, the model of Ross and Howell predicts higher *S. fragilissima*
572 habitat suitability around the slopes of Edoras and Fangorn banks and along the slopes of the
573 Porcupine Seabight and Goban Spur relative to the model presented in this paper. In addition, the
574 model presented in this paper predicts larger areas of high habitat suitability, relative to Ross and
575 Howell (2012), for *S. fragilissima* to the south of the Wyville-Thomson Ridge, between Bill Bailey's
576 Bank and Rosemary Bank, and in the Hatton-Rockall Basin. The overall similarity of the two models,
577 however, gives further confidence to their predictions, especially so considering that they are
578 produced from different data sets - Ross and Howell choosing only to use topographic data.

579 Choice of modelling resolution is an important factor when producing predictive species distribution
580 models (Guisan *et al.* 2007). While higher resolution outputs are preferable when we need to
581 capture environmental variability at small spatial scales (like the rapid changes in temperature that
582 occur with distance across the Faroe-Shetland Channel (Oey, 1997)) and for visualising predictions,
583 they do carry certain associated error and limitations (Davies *et al.* 2008; Davies and Guinotte,
584 2011). Since, other than depth, global environmental layers are not available at 30 arc-second
585 resolution, variables have to be up-scaled from their native resolution to that required (30 arc-
586 seconds in this analysis - see Methods). Up-scaling inevitably introduces some error, with this error
587 growing as the difference between native and required resolution increases (Davies and Guinotte,
588 2011). Examples of the manifestation of this error include the generalisation and smoothing of
589 variables and the failure to incorporate small scale variability in the up-scaled layers that is not
590 present in the lower resolution source data (Davies and Guinotte, 2011; Rengstorf *et al.* 2012).
591 Further, the majority of global layers currently available that can be up-scaled represent annual
592 means of values (in order to ensure a high number of samples to maximise certainty in the variables
593 (Davies and Guinotte, 2011)). As a result, these layers do not capture any component of annual
594 variability, a particular drawback when modelling highly seasonal high latitude regions. However,
595 comparison of up-scaled data with GLODAP (Global Ocean Data Analysis Project) test bottle water

596 data by Davies and Guinotte (2011) found the two datasets to be highly correlated, and hence the
597 authors concluded that any issues associated with the up-scaling method are outweighed by its
598 benefits.

599 Whilst the dataset utilised in this study comprised a high number and diversity of variables, there
600 were still variables which may have been informative but were not available for use. Chief amongst
601 these were productivity variables, such as measures of particulate organic carbon reaching the
602 seafloor, and surface water chlorophyll a concentrations. These variables were not available for use
603 owing to a rapid decline in data quality at latitudes greater than $\sim 70^\circ$ (see section 2.2). Substratum
604 type is a further variable that would have been interesting to incorporate into this analysis as there
605 is evidence for sediment-type preference in xenophyophores (Levin and Thomas, 1988).

606 Unfortunately, a global environmental layer containing details of sediment type is not yet
607 available, but progress is being made towards this goal (e.g. Shumchenia and King, 2010).

608 Furthermore, the hydrodynamic variables used in this study under-performed and were not of
609 sufficient sensitivity to capture local scale variation in flow rates associated with isolated
610 topographic features such as seamounts. Thus, considering the current uncertainty surrounding
611 xenophyophore feeding methods, it would be particularly interesting to incorporate a high
612 resolution local current flow into future analyses. Such a layer is currently unavailable at a global
613 scale, although advances are being made at the regional scale (Mohn *et al.* 2014).

614 Potential evidence for xenophyophore sampling bias has been mentioned in section 3.1. Firm
615 evidence of sampling bias would imply that the current distribution of presence localities used in
616 this study is not adequate to represent all potential environments from which xenophyophores can
617 be sampled. This would potentially lead to false negatives in the Maxent outputs. Whether this is
618 the case will only become apparent following further sampling and analyses.

619 The most conclusive way to validate or refute the predictions of this analysis (Figures 3-5) would be
620 to directly test them in the field via 'ground-truthing' (Guinotte and Davies, 2012). Do we find
621 xenophyophores in areas of predicted high habitat suitability that have not yet been sampled, like
622 the Andaman Sea, or do these predictions represent false positives? There are some issues with this
623 method. Assuming that a cruise to undertake this task could be funded, it would be a huge
624 undertaking to systematically search an entire 30 arc-second cell of high predicted habitat

625 suitability using ROVs or camera equipment, and subsampling may miss specimens as
626 xenophyophore distributions may be patchy within this cell. However, it should be noted that
627 xenophyophores have been recorded at very high densities in areas of suitable habitat (Tendal and
628 Gooday, 1981), increasing the likelihood of discovery.

629 Finally, although species distribution modelling has progressed rapidly in recent years in terms of
630 resolution (compare the results of Davies *et al.* (2008) with those of Davies and Guinotte (2011) and
631 Yesson *et al.* (2012)) and model performance criteria (e.g. Warren and Seifert, 2011), clearly the
632 availability of additional relevant environmental variables with global coverage at high resolution,
633 and a growing number of reliable presence localities will continue to lead to ever an increasing
634 accuracy of models suitable for a number of research and industrial applications.

635

636 4.4 Conclusive remarks

637 This study represents the first of its kind for xenophyophores at a global scale and serves to
638 improve knowledge of their distributions and further illuminate details of their ecology.
639 Additionally, this analysis draws attention to the possible use of these fragile and remarkable deep-
640 sea megafaunal ecosystem engineers in enhancing MPA planning and designation. However, this
641 work represents but a first step and aims to motivate continued research into these intriguing and
642 important organisms; testing model predictions with further sampling, performing local-scale high-
643 resolution analyses and addressing some of the still unanswered questions concerning
644 xenophyophore ecology and physiology.

645

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