

1 **LIKE A ROLLING STONE: THE MOBILITY OF MAERL (CORALLINACEAE) AND**  
2 **THE NEUTRALITY OF THE ASSOCIATED ASSEMBLAGES**

3  
4 GUSTAVO HINOJOSA-ARANGO<sup>1</sup>, CHRISTINE A. MAGGS, MARK P. JOHNSON<sup>2\*</sup>

5  
6 *School of Biological Sciences, Queen's University Belfast, 97 Lisburn Road,*

7 *Belfast, Northern Ireland, BT9 7BL.*

8  
9 \*Corresponding author: Tel.: +353 91 492325, fax: +353 91 525005

10 *e-mail address:* mark.p.johnson@nuigalway.ie

11  
12 <sup>1</sup>Present address: Boston University Field Center, Baja California Sur, Mexico

13 <sup>2</sup>Present address: Martin Ryan Institute, National University of Ireland, Galway, University  
14 Road, Galway, Ireland

15 *Abstract.* Beds of non-attached coralline algae (maerl or rhodoliths) are widespread and  
16 considered relatively species rich. This habitat is generally found in areas where there is  
17 chronic physical disturbance such that maerl thalli are frequently moved. Little is known,  
18 however, about how natural disturbance regimes affect the species associated with maerl. This  
19 study compared the richness, animal abundance and algal biomass of maerl-associated species  
20 over a two year period in a wave disturbed and a sheltered maerl bed. Changes in associated  
21 species over time were assessed for departures from a neutral model, where the dissimilarity  
22 between samples reflects random sampling from a common species pool. Algal biomass and  
23 species richness at the wave exposed site and on stabilized maerl at the sheltered site were  
24 reduced at times of higher wind speeds. The changes in species richness were not  
25 distinguishable from a neutral model, implying that algal species were added at random to the  
26 assemblage as the level of disturbance lessened. Results for animal species were more mixed.  
27 Although mobile species were less abundant during windy periods at the exposed site, both  
28 neutral and non-neutral patterns were evident in the assemblages. Artificial stabilization of  
29 maerl had inconsistent effects on the richness of animals, but always resulted in more attached  
30 algal species. While the results show that the response of a community to disturbance can be  
31 neutral, the domain of neutral changes in communities may be relatively small. Alongside non-  
32 neutral responses to natural disturbance, artificial stabilization always resulted in an  
33 assemblage that was more distinct than would be expected under random sampling from a  
34 common pool. Community responses to stabilization treatments did not consistently follow the  
35 predictions of the dynamic equilibrium model, intermediate disturbance model or a facilitation  
36 model. These inconsistencies may reflect site-specific variation in both the disturbance regime  
37 and the adjacent habitats that provide source populations for many of the species found  
38 associated with maerl.

39

40 *Key words:* Stability; *Phymatolithon calcareum*; *rhodolith*; disturbance, nestedness

## INTRODUCTION

41  
42 Maerl beds formed by free living coralline algae (also known as rhodolith beds) are  
43 widespread marine biogenic habitats with a high conservation importance (Foster 2001). Maerl  
44 are habitat forming ‘foundation species’ (Dayton 1972, Bruno and Bertness 2001): by virtue of  
45 the branching and interlocking nature of their thalli, a complex three-dimensional habitat is  
46 constructed. Disturbance is also a key feature of maerl beds as individual thalli can be moved  
47 by waves, currents or bioturbation (Steller and Foster 1995, Harris et al. 1996, Marrack 1999).  
48 Although maerl beds appear to support a relatively high diversity, little is known about the  
49 interactions among the associated species (Foster 2001).

50 It is possible that the natural patterns of disturbance in maerl beds affect the associated  
51 biodiversity (more is known about the effects of anthropogenic disturbances, Hall-Spencer and  
52 Moore 2000, Hauton et al. 2003, Hall-Spencer et al. 2006). In the context of community  
53 ecology, disturbance is often linked to patterns of species diversity. A well known case is the  
54 intermediate disturbance hypothesis (IDH, Connell 1978), which proposes a unimodal  
55 relationship between disturbance and diversity with the highest species richness under  
56 intermediate disturbance. A related theory is Huston’s (1979) dynamic equilibrium model  
57 (DEM, see also Kondoh 2000), which modifies the relationship between disturbance and  
58 diversity according to productivity. For example, under low productivity diversity decreases  
59 monotonically with disturbance as the resource-limited conditions where competitive  
60 displacement occurs are never reached. Most theoretical explanations for the IDH and DEM  
61 are based on trade-offs between the ecological traits of species, generally invoking a  
62 competitive hierarchy (Petraitis et al. 1989, Kondoh 2000). There are two contrasting  
63 alternatives to the idea that competitive interactions underlie disturbance-diversity  
64 relationships. A simulation model is used by Kadmon and Benjamini (2006) to demonstrate  
65 that neutral theory can produce disturbance-diversity relationships without invoking  
66 differences in ecological traits among species. A non-neutral alternative is that facilitation by

67 foundation species may override competitive exclusion (Bruno and Bertness 2001). The  
68 mechanism for this facilitation effect relates to the situation where a foundation species  
69 constructs a more complex habitat under conditions of low disturbance. Greater habitat  
70 complexity can lead to a greater surface area and a greater level of heterogeneity (Johnson et  
71 al. 2003). Greater surface area and heterogeneity can dilute the strength of competitive  
72 interactions (Petren and Case 1998), causing species diversity to monotonically increase as  
73 disturbance decreases. The aim of the current study was therefore to evaluate negative, neutral  
74 and positive interactions in the response of maerl associated species to the natural range of  
75 disturbance.

76 There are a number of practical issues in evaluating the responses of a community to a  
77 gradient of disturbance. Correlational studies require a sufficiently broad range of disturbances  
78 to have occurred for a signal to be apparent from observational noise. Experimental  
79 manipulations can be hampered by the use of inappropriate disturbance scales, or the use of  
80 discrete treatments along a continuum of natural disturbances may obscure detection of the  
81 underlying relationship (Kimbrow and Grosholz 2006). The current study attempted to address  
82 these shortcomings by combining observational studies of maerl beds under different  
83 environmental conditions (wave or tides as the dominant hydrodynamic disturbance) with an  
84 experimental stabilization of maerl. Tying maerl thalli down was used to investigate the  
85 consequences of artificially shifting the observational window towards the more sheltered  
86 extreme of the disturbance continuum. Increased wind speeds were hypothesized to disturb the  
87 maerl assemblages, resulting in lower abundances and lower species diversities. Disturbances  
88 are hypothesized to affect abundances more on free maerl than on tied maerl. Dependant on the  
89 shape of the disturbance-species richness curve, this will result in higher or lower numbers of  
90 species on tied treatments when compared to free maerl.

91 At small spatial scales, the assemblages on maerl beds are likely to be open: recruits will  
92 come from a wide area rather than through local reproduction. The composition of the regional

93 species pool (metacommunity, Hubbell 2001) in immigration-dominated assemblages such as  
94 this can be estimated from the average species abundance distribution across all samples.  
95 Hubbell's neutral theory therefore emphasizes the relative abundances of species in addition to  
96 the accumulated inventory at the scale in question. In a neutral assemblage differences in  
97 species composition along a gradient of disturbance should be no greater than the differences in  
98 composition between random samples from the regional species pool (Kadmon and Benjamini  
99 2006). The appeal of neutral theories is that tractable generalizations may be possible without  
100 the need for detailed species specific information. In contrast, the IDH and DEM models  
101 emphasize the importance of species traits: species are more likely to be found at particular  
102 disturbance frequencies due to being, for example, competitive dominants or superior colonists.  
103 Hence under IDH and DEM, species assemblages at different levels of disturbance are likely to  
104 be more dissimilar than expected when compared to a random selection from the regional pool.

105 The DEM and neutral theory (Kadmon and Benjamini 2006) can be used to explain both  
106 monotonic and monomodal species richness-disturbance relationships. The IDH is monomodal  
107 with lower richness at low levels of disturbance, while facilitation models predict higher  
108 species richness at low disturbance (Bruno and Bertness 2001). Randomization tests can be  
109 used to test whether differences between tied and free assemblages are neutral or suggest that  
110 species traits are important. If species traits are important in the turnover of species between  
111 free and stabilized maerl, this is relevant to maerl conservation as it indicates that the  
112 community will change in response to altered hydrological regimes. It is not possible, however,  
113 to distinguish between some of the mechanisms responsible for any differences between tied  
114 and free communities. While facilitation and IDH have opposing predictions, the DEM would  
115 be consistent with either higher or lower richness on stabilized maerl.

116 The three dimensional matrix of a maerl beds is probably a greater resource for animals  
117 than it is for algae, which depend on light falling on the upper surface of the bed. This may  
118 result in algae having a lower net benefit from stabilization of maerl and a higher likelihood of

119 interspecific competition. In addition, many maerl associated species are found in adjacent  
120 habitats (Birkett et al. 1998). This may lead to mobile animals moving in and out of the maerl  
121 matrix with changing disturbance. Data from the current study were therefore analyzed  
122 separately for mobile animals, sessile animals and algae to test whether neutral responses to  
123 disturbance were more common in the assemblage of mobile animals.

124

## 125 **METHODS**

### 126 *Study system*

127 Maerl beds occur from the lowermost intertidal zone to depths of over 100 m (Littler et al.  
128 1991). The ecological importance of maerl habitats is recognized by, for example, listing of  
129 maerl species in the European Union's Habitats Directive (92/43/EEC). Maerl beds are  
130 reported to support richer communities than habitats of equivalent grain size such as gravel or  
131 shell bottoms (Cabiocch 1969, Keegan 1974). Causes of the relatively high species diversity in  
132 maerl beds are unclear (Foster 2001). The three-dimensional structure of maerl beds is likely to  
133 increase surface area and habitat diversity, both of which may facilitate greater species  
134 coexistence.

135 Hydrodynamics play a key role in the distribution, shape, branching pattern and stability of  
136 maerl thalli (Bosence 1976, 1985, Steneck 1986, Hily et al. 1992, Steller and Foster 1995,  
137 Basso 1998). Maerl beds do not develop if water movement is so slight that beds are covered  
138 by sediment or where water movement is too high, leading to destruction or unsustainable loss  
139 rates of thalli (Foster 2001). In between these extremes of water movement, periodic rotation is  
140 necessary for maerl as it allows light to reach all sides of the thalli and retards burial and  
141 fouling (Steneck 1986). Such periodic rotation represents a potential disturbance event to  
142 species associated with maerl. During turnover events, attached flora and fauna could be  
143 abraded or buried on the underside of maerl thalli and motile fauna impacted by abrasion  
144 between thalli. Such disturbances are frequently seen as preventing the development of a stable

145 community (Menge and Sutherland 1976, Ebeling et al. 1985, Maughan and Barnes 2000). A  
146 further effect of thallus movement is that the habitat may become less structurally complex,  
147 due to breakage of more complex thalli and the loss of habitat heterogeneity as, on average,  
148 more thalli experience the same conditions as opposed to persistent differentiation between  
149 surface and buried thalli.

150 Experiments were carried out between May 2002 and April 2004 at two maerl beds in  
151 Strangford Lough, a bay on the east coast of Northern Ireland which is a marine nature reserve  
152 and a Special Area of Conservation (SAC) under the EC Habitats Directive. One of the beds  
153 (Sketrick Island) is formed from fossil maerl deposits. Maerl at Sketrick Island (Appendix A)  
154 is found between the intertidal and 5 m depth below chart datum (the height of the lowest  
155 astronomical tide), covering 80% or more of the seabed. The maerl bed consists primarily of  
156 subfossil *Lithothamnion glaciale* Kjellman mixed with sparse live *Phymatolithon calcareum*  
157 (Pallas) Adey & McKibbin. As this bed is in the channel between Sketrick Island and the  
158 mainland it is generally protected from wave action. Tidal currents in the Sketrick Channel can  
159 reach velocities of up to  $2.57 \text{ m s}^{-1}$  (Brown 1990). The second bed, Zara Shoal, is made up of  
160 live maerl, predominantly *Phymatolithon calcareum*, occupying up to 90% of the total area.  
161 The Zara bed is deeper than maerl at Sketrick, lying between 5 and 9 meters depth. Both beds  
162 consist of a fairly thin cover of maerl (one to two layers of thalli) overlying a mixture of coarse  
163 and fine sediment (with a greater proportion of fine material at Sketrick). The habitats around  
164 each bed consist of mosaics of rock, fine and coarse sediment and include other biogenic  
165 features (circalittoral Kelps and *Modiolus modiolus* reefs).

166 As the studied beds are relatively shallow, they are susceptible to disturbance from  
167 wind-generated waves. The shelter at Sketrick prevents much wave activity, but Zara is more  
168 affected by wind-driven waves. In the study by Davies and Johnson (2006), shores adjacent to  
169 the Sketrick bed were in the most sheltered quartile of sites around the shores of Strangford  
170 Lough, while the shores closest to Zara were in the most exposed quartile of sites. Marrack

171 (1999) estimated that wind speeds in excess of  $6 \text{ m s}^{-1}$  for periods over 4 hours would move  
172 thalli at depths of 4-5 m in the Isla el Requesón bed off Baja California. Average daily wind  
173 speeds in Strangford are generally greater than those at the Isla el Requesón. On average there  
174 were 16 days each month at Strangford with a wind speed exceeding  $6 \text{ m s}^{-1}$  during the period  
175 when experiments were carried out (Fig. 1). Such frequencies are comparable to the winter  
176 month data in Marrack (1999), where movement of thalli was observed to be 'frequent'. At the  
177 scale at which experiments were carried out (see below) there was no evidence for seasonality  
178 in wind speeds at Strangford. For example, the highest average daily wind speed was observed  
179 in March 2003, but March 2004 had one of the lowest mean wind speeds. Average daily wind  
180 speed and frequency of days with average speeds  $> 6 \text{ m s}^{-1}$  were highly correlated ( $r = 0.853$ ,  $p$   
181  $< 0.001$ ). There was no pattern of autocorrelation in the wind time series. The autocorrelation  
182 at a 2-month lag was 0.067 and the Ljung-Box Q statistic for lags up to 6 was 7.663 (not  
183 significant against  $\chi^2$  distribution, df 6, no significant lags). Tidal currents can also move maerl  
184 thalli, but the variation among separate two-month experimental periods at Strangford was low  
185 (coefficient of variation for maximum tidal range 7%). Tides are likely to represent a continual  
186 background amount of thallus movement with little variation over time.

187

### 188 *Experimental treatments*

189 Maerl were artificially stabilized at the two beds in Strangford Lough to examine the  
190 effects of reduced mobility on the assemblage of associated species. Many variables are likely  
191 to vary between the live and dead maerl beds. Such factors confound a simple comparison of  
192 the two beds so the experimental design does not therefore formally compare the beds and the  
193 main analyses presented (on neutrality) are not dependent on a comparison between beds.  
194 Variation in average daily wind speed was used as a covariate to test for changes in community  
195 structure associated with disturbance. Increasing wind speeds were predicted to cause lower  
196 species diversities and abundances due to the disturbance of thallus movement. If competitive

197 interactions and trade-offs are important, then species were expected to be added non-randomly  
198 to treatments as wind speed decreased. Higher abundances of animals and biomass of algae  
199 were predicted for stabilized treatments. If competitive exclusion becomes important within the  
200 scales investigated then evidence for a unimodal relationship between diversity and disturbance  
201 or a lowered species diversity in stabilized versus free replicates was predicted (IDH).

202         Stabilization treatments involved individually tying thalli onto 15 x 15 cm plastic  
203 meshes until meshes were completely covered by a single layer of thalli (Appendix B).  
204 Experiments at the Zara Shoal bed used live thalli of *Phymatolithon calcareum*, while dead  
205 *Lithothamnion glaciale* maerl thalli from Sketrick were deployed at the Sketrick Island bed.  
206 Meshes for each sampling period ( $n = 3$ ) were tied out onto separate  $0.25 \text{ m}^2$  paving slabs,  
207 placed 6 m below Chart Datum at Zara Shoal and 3 m below CD at Sketrick Island. Slabs were  
208 placed 5 m apart within each maerl bed.

209         Plastic meshes without maerl were used to examine the development of the  
210 assemblages in the absence of maerl. Colonization of these empty plastic meshes was minimal.  
211 A maximum of 20 organisms (rarely algae) comprising no more than five species was recorded  
212 following two months of exposure. This compares to over 20 species and 400 individual  
213 animals on average in tied maerl treatments. The presence of a mesh was not, therefore,  
214 considered to add a large artifact to the observed assemblages in tied treatments.

215         Meshes were attached by plastic ties to the concrete paving slabs for 12 bimonthly  
216 intervals from May 2002 to April 2004. A period of two months was used for stabilizing maerl  
217 as this period represents close to the maximum time that beds will be undisturbed, based on the  
218 frequency of windy days (Fig. 1). Meshes were retrieved at the end of each 2-month exposure,  
219 with each mesh cut free and carefully placed in labeled plastic bags underwater to restrict  
220 washout of associated organisms.

221         Species associated with stabilized maerl were compared to specimens collected from 3  
222 quadrats of natural, free-moving maerl. These samples were collected by placing a plastic cage

223 15 x 15 x 4 cm haphazardly over the maerl bed, in the same area where concrete blocks had  
224 been placed. The underside of the cage was sealed by sliding a plastic sheet underneath, with  
225 enclosed material transferred carefully to labeled plastic bags. Replicates of 'free' maerl were  
226 therefore of the same dimensions and thickness as stabilized treatments. A total of 12 sampling  
227 dates resulted in the collection of 72 samples at each maerl bed (36 artificially stabilized maerl  
228 and 36 free maerl quadrats).

229

### 230 *Sample processing*

231 Attached macroalgae were removed from the samples with aid of forceps and identified  
232 to species wherever possible. Only crustose algae and erect thalli bigger than 5 mm were  
233 processed due to difficulties in unambiguously identifying smaller individuals. Epifaunal  
234 organisms entangled with algal thalli were removed and blotted dry weights of all included  
235 algae were measured on a digital weighing scale with a precision of 0.01 g.

236 Following removal of algal material, samples were fixed in 4% formalin-seawater and  
237 preserved in a 70% alcohol solution. Sessile organisms such as ascidians, sponges and some  
238 molluscs were removed using forceps. Samples were shaken to remove vagile organisms with  
239 the alcohol solution from each sample sieved through a 0.5 mm mesh to collect fauna. The  
240 retained sediment was sorted under a binocular dissecting microscope to extract any remaining  
241 organisms. Epifauna was identified to species, genus or to the best resolution possible. Due to  
242 the difficulties in recognizing individuals of encrusting colonial invertebrates, these groups  
243 were counted as one individual for each maerl piece they were attached to. Counts for these  
244 species may therefore under-represent the number of separate colonization events.

245

### 246 *Statistical analyses*

247 Species richness was calculated for each replicate for both algae and animals. Due to  
248 difficulties in unambiguously identifying individual algae and the wide variation in thallus

249 sizes, total abundance of individuals was only calculated on the basis of counted animal  
250 species. The equivalent variable for algae was total dry mass of attached fronds. All response  
251 variables were compared between stabilized (tied) and free maerl treatments using ANCOVA,  
252 with average daily wind speed during the relevant 2-month exposure period as the covariate.  
253 Homogeneity of slopes was assessed for each treatment against wind speed ANCOVA by  
254 fitting a full model that included the treatment x wind speed interaction. A significant  
255 interaction implies that the rate of change in a response variable with respect to wind speeds  
256 differs between treatments: the slopes are heterogeneous. In this case results are presented  
257 using the separate slopes for each treatment. Where the interaction was not significant,  
258 homogeneity of slopes was assumed and results are presented from a simple (no interaction  
259 fitted) ANCOVA model with parallel slopes in the different treatments (Quinn and Keough  
260 2002). Results from the simple model are presented as two parallel lines or a single line,  
261 depending on the significance of the treatment effect. Non-significant results for the covariate  
262 are presented without a slope; just the mean for each treatment is used. Assumptions of  
263 linearity and heterogeneity of variances were examined using residual plots. There was no  
264 evidence of the systematic deviation from random scatter that might be associated with non-  
265 linearity or heteroscedasticity in the data for species richness. Algal biomass and animal  
266 abundances required logarithmic transformation to produce acceptable patterns in the residuals.

267         Changes in the overall structure of assemblages were evaluated with multivariate  
268 techniques. Systematic variation in assemblage structure with changing wind speeds was  
269 assessed by calculating the non-parametric correlation between a similarity matrix based on  
270 multivariate distances between the replicates (Sørensen coefficient) and a similarity matrix  
271 between dates based on average wind speed. Positive correlations between wind and species-  
272 based distance matrices imply that periods of different wind speed have different assemblages.  
273 Such differences could be due to species' responses to disturbance and patterns arising from  
274 other ecological traits such as competitive ability. However, a correlation between distance

275 matrices could be produced simply by changes in abundance among replicates. This occurs as  
276 measures of assemblage similarity are generally affected by both the numbers of species found  
277 in either replicate as well as the number of species in common (Koleff et al. 2003). To derive  
278 an expectation for the correlation between matrices under an assumption of neutrality a  
279 resampling algorithm was set up in PopTools (Hood 2006). An abundance distribution was  
280 calculated for each combination of treatment and site based on the average abundances of each  
281 taxon across all dates. Individuals were selected with probabilities based on their relative  
282 abundances. For example the most common species may be 40 times more likely to be picked  
283 than the rarest species. As replicates had different total abundances this involves 36 (12 dates  
284 by three replicates) separate random selections of individuals. For illustration, simulations for  
285 mobile species on free maerl at Zara involved picking between 18 and 468 individuals from the  
286 relative abundance distribution. Correlation between the wind distance matrix and the distance  
287 matrix based on pairwise comparisons of the 36 random selections therefore provides an  
288 estimate of association between a neutral assemblage and wind speed. Mean and confidence  
289 limits for the neutral model were estimated by making 499 separate sets of random selections.  
290 As algae were not counted individually, the relative abundance distribution was based on  
291 average frequency of occurrence. The appropriate number of individuals to pick from the algal  
292 species pool so that the observed number of species per replicate was matched was found by  
293 simulation.

294         The neutral model as tested here has some similarities with tests of ‘nestedness’  
295 (Patterson & Atmar 1986). When communities are nested, the compositions of less rich  
296 communities form subsets of richer communities. A neutral model will form this pattern as the  
297 relatively abundant species will be in most samples while rarer species will only occur in  
298 communities with high numbers of individuals or biomass. This mechanism is recognized in  
299 the nestedness literature as ‘passive sampling’ (Cutler 1994, Higgins et al. 2006, Ulrich and  
300 Gottelli 2007). The nestedness literature has frequently used null models to test for nestedness

301 that rely on stochastic placement of species rather than individuals (Higgins et al. 2006). This  
302 means that the available software is not generally suitable for tests of a neutral model. A  
303 second distinction between the approach in the current study and the nestedness literature is  
304 that calculations of nestedness generally rank samples by species richness. The tests of  
305 disturbance presented here make a more explicit hypothesis by testing for nested structure  
306 along a proposed gradient of disturbance (wind stress). The neutral model tested in this study is  
307 therefore a more explicit hypothesis than existing tests of nestedness. Measurements of  
308 nestedness should, however, be consistent with our analyses. Matrix ‘temperatures’ were  
309 therefore calculated for all taxon matrices using the methods in Ulrich and Gotelli (2007);  
310 where progressively stronger nesting results in a lower matrix temperature. The matrix  
311 temperature is an analogy to thermodynamics, but as a ratio it does not have units of  
312 measurement.

313         The assemblages on free and stabilized maerl were also compared using random  
314 selections from a common species pool to test for neutrality. Differences in mean abundance  
315 would cause differences between the two treatments even if replicates had sampled the same  
316 underlying species pool. The ANOSIM test statistic (R) was used to compare between  
317 assemblages on tied and stabilized maerl. This statistic is based on subtracting the average rank  
318 similarity within treatments from the average rank similarity between treatments (Clarke 1993).  
319 An expected value for the ANOSIM statistic under neutral selection from the species pool was  
320 derived using PopTools. Individuals were selected based on probabilities in the relative  
321 abundance distribution for tied and free replicates combined. The ANOSIM test statistic was  
322 then calculated for these neutral selections based on the number of individuals in each of the 72  
323 replicates. As before, this procedure was repeated to derive an expected mean ANOSIM  
324 statistic and confidence intervals under an assumption of neutral selection from the available  
325 species pool.

326

## RESULTS

327  
 328 There was substantial overlap between the species recorded on tied and free maerl. At Sketrick  
 329 there were 91 animal species on tied maerl and 102 on free maerl, with 75 of these species in  
 330 common. There were slightly more algal species in total on tied maerl (21) than there were on  
 331 free maerl (18). A total of 14 species were shared between tied and free maerl. Similar species  
 332 richness patterns were found at Zara Shoal, although the overall species numbers were slightly  
 333 higher than at Sketrick. A total of 105 animal species and 26 algal species were recorded from  
 334 tied treatments, with 120 animal species and 20 algal species on free maerl. The different  
 335 treatments at Zara had 86 animal species and 20 algae in common.

336 The most common animal species were amphipods. The most frequently counted  
 337 species at Sketrick were *Corophium sextonae* Crawford, *Aora typica* Krøyer, *Lysianassa*  
 338 *ceratina* Walker, *Cheirocratus sundevallii* (Rathke) and the bivalve *Crenella decussata*  
 339 (Montagu). *A. typica* and *L. ceratina* were also among the most abundant animal species at  
 340 Zara, along with *Microdeutopus versiculatus* (Bate), the isopod *Janira maculosa* Leach and the  
 341 bivalve *Mytilus edulis* L. The most frequently recorded algae (in over 50% of replicates) were  
 342 *Corallina officinalis* L., *Dictyota dichotoma* (Hudson), *Peyssonnelia dubyi* Crouan & Crouan  
 343 and *Ulva lactuca* L. at Sketrick; *Plocamium cartilagineum* (L.) Dixon, *P. dubyi* and  
 344 *Stenogramme interrupta* (C. Agardh) Montagne ex Harvey at Zara Shoal.

345

### 346 *Effects of maerl mobility on assemblages*

347 Wind speed affected algal and animal abundances at Zara (Table 1, Fig. 2). Algal  
 348 biomass and mobile animal abundances were lower under more windy conditions. The  
 349 abundance of sessile species at Zara actually increased with wind speed. These patterns were  
 350 not evident at the more sheltered site. Algal biomass on tied maerl at Sketrick was, however,  
 351 lower under higher wind speeds. The fitted slope for algal biomass on free maerl at Sketrick  
 352 was not significantly different from zero (slope 0.1270 (SE 0.1262),  $t = 1.01$ , not significant).

353 The disturbance associated with higher wind speeds did not affect animal species  
354 richness (Table 2). In contrast, algal species richness fell with increasing wind speeds (Fig. 3).

355 Cases where wind speed appeared to be affecting the abundance or biomass of  
356 assemblages were examined for evidence of non-neutral changes in assemblages. In most cases  
357 the measured association between species based distance matrices and the wind speed distance  
358 matrix were within the confidence limits of a neutral model. Changes in assemblages were no  
359 more structured than would be expected with random selection of species from the available  
360 pool (Table 3). Free maerl treatments at Zara were an exception to this pattern. The association  
361 between wind speed and assemblages matrices in these cases was higher than the upper  
362 confidence interval. There was greater discrimination between assemblages at different wind  
363 speeds than might be expected from neutrality.

364 Calculated matrix temperatures were consistent with the results from the more explicit  
365 test for association with wind speed. The two treatments that significantly departed from a  
366 neutral response to wind disturbance had the lowest degree of nesting (temperatures greater  
367 than 18). As would be expected under passive sampling, experimental treatments that  
368 conformed to a neutral model had lower matrix temperatures (range 5 – 13).

369

#### 370 *Differences among experimental treatments*

371 Stabilizing maerl always increased algal species richness with respect to free maerl.  
372 The results for animals are more mixed (Table 2). Both mobile and sessile animal groups were  
373 less species-rich on stabilized maerl than on free maerl at Zara. Tying maerl down resulted in  
374 the opposite effect with mobile animal species at Sketrick and no difference in richness among  
375 treatments for sessile species at this site.

376 The assemblages on tied and free maerl differed more than would be expected under a  
377 neutral model. The dissimilarities between treatments were not solely due to sampling different  
378 numbers of individuals from a common species pool (Table 4). The hypothesis of neutrality

379 between treatments could therefore be rejected with species-specific ecology invoked to  
380 explain the different assemblages found on tied and free maerl.

381

## 382 **DISCUSSION**

### 383 *Neutrality and responses to disturbance*

384 High wind speeds affected the abundance of animals and biomass of attached algae at  
385 the more exposed site and the biomass of algae on tied maerl at Sketrick. In all cases except  
386 that of sessile species at Zara, high wind speeds were associated with lower  
387 biomass/abundance, as would be expected if wind-driven waves were disturbing the maerl  
388 beds. The response of algae to increased wind speeds gives a clear example of how  
389 disturbances can affect biomass and species richness but with the changes in assemblage  
390 structure following a neutral model. There was no evidence that particular algal species were  
391 more prevalent at any point along the spectrum of disturbances. If this were the case there  
392 would be greater dissimilarities between replicate assemblages than was observed. Algae on  
393 maerl are therefore an example of the 'more individuals' process (Kadmon and Benjamini  
394 2006) in which species are added to an assemblage as biomass increases, but they are not  
395 added in any particular order.

396 The neutral model was not, however, universally applicable to results. Disturbance by  
397 higher winds was associated with lower abundances of mobile animals on free maerl at Zara.  
398 Species assemblages on free maerl at Zara were, however, more distinct at different wind  
399 speeds than would be expected from random sampling of the same species pool. Under a  
400 neutral model, all mobile species would be expected to have negative correlations with wind  
401 speed as overall abundance also decreases under windier conditions. The most extreme  
402 departures from this pattern were species either insensitive to wind speed or showing slight  
403 increases in abundance with wind speed. For example, *Hydrobia neglecta*, *Achelia longipes*  
404 and *Ophiura albida* all had correlations with wind speed exceeding 0.24. The rejection of

405 neutrality suggests that these species are more likely to colonize maerl under windier  
406 conditions or they may be excluded by ecological interactions at low wind speeds. The same  
407 species were more common in free maerl than in stabilized treatments, which is consistent with  
408 some preference for a more mobile substratum.

409         It is not entirely clear why the neutral model may be applicable in some situations and  
410 not others. The hypothesis that algae may be more likely to have asymmetric competitive  
411 interactions was not supported by the analysis. If asymmetric ecological interactions are  
412 involved in the changes in assemblages, then one might expect such interactions to be more  
413 evident under higher abundances as resources are more likely to be limited and encounter rates  
414 are likely to be higher. This is the case for mobile species on free, as compared to stabilized,  
415 treatments at Zara. This explanation is not, however, consistent with the equal abundances in  
416 tied (neutral) and free (structured) sessile assemblages at Zara. Although, if tied maerl is  
417 accepted as a more heterogeneous and complex environment, the effective surface area for  
418 attachment may be higher than is the case in free maerl even at the same overall abundance.

419

#### 420                                   *Disturbance-diversity relationships*

421         The relationships between disturbance and species richness were varied. Only algal  
422 species richness was associated with variation in wind speed. This pattern was consistent with  
423 the neutral interactions leading to the pattern predicted under the DEM with low productivity  
424 (increased biomass and species richness under low disturbance). Within the timescale of the  
425 experiment there was no evidence for a reduction in algal species richness under low  
426 disturbance. Either the biomass where competitive exclusion is important is not reached, even  
427 on stabilized maerl, or there are facilitation effects that offset any competitive exclusions  
428 (Bruno and Bertness 2001). Variable wind speeds had no effect on mobile or sessile animal  
429 species richness. Stabilization was proposed to cause a reduction in disturbance and an  
430 opportunity for the number of individuals and species to increase relative to free maerl.

431 Richness in stabilized maerl was, however, found to be equal to, lower or higher than on free  
432 maerl, depending on species' mobility and site. Results from Zara suggest that increasing  
433 stability of maerl will result in lower species numbers. This may be due to lower numbers of  
434 individuals (mobile species) or due to other changes in the assemblage, potentially including  
435 competitive interactions (sessile species). Similarly, the pattern for mobile species richness at  
436 Sketrick follows the increased abundance of individuals on stabilized maerl. Associations  
437 between the relative abundances and species richness counts between treatments are consistent  
438 with the facilitation hypothesis or the DEM. IDH was generally not supported, at least over the  
439 time scales of experiments. It may be that competitive dominants can only depress species  
440 numbers over longer timescales.

441

#### 442 *Differences between sites and treatments*

443 Although a wider range of sites is required to control for potential confounding factors,  
444 the absence of a wind effect at Sketrick is consistent with the sheltered nature of this site.  
445 Continual disturbance by tidal currents is probably reflected in the greater mean richness in tied  
446 versus free treatments for mobile species and algae at Sketrick. Only by tying down maerl does  
447 the biomass of attached algae become sensitive to wind speed at Sketrick.

448 Although many species were shared between tied and free maerl, the differences  
449 between treatments were greater than expected under a neutral model. This implies that,  
450 regardless of the pattern in species richness, changes in maerl mobility are likely to change the  
451 nature of the associated community. The size of the experimental treatments may have  
452 underestimated the effect of stabilizing an entire bed, unfortunately future investigations of  
453 such scale dependant effects are complicated by issues including the logistics of stabilizing  
454 large areas of a protected habitat.

455 The presence of adult molluscs and crustaceans in stabilized maerl indicates that  
456 migration of mobile fauna is common. Migrations of sessile fauna are also possible. The

457 category of 'sessile' in this study included bivalves, and this group numerically dominated  
458 counts of sessile species (average 90.3% (SE 1.04) of all counted individuals). Bivalves, while  
459 not as mobile as crustaceans, are not permanently attached (Ansell 1969). The response of  
460 sessile animals (increase in abundance at Zara) to increased wind speeds may indicate  
461 immigration from more disturbed environments into maerl. Alternatively, maerl may not be a  
462 favored habitat when disturbance is low, perhaps due to siltation.

463         The idiosyncratic results for both neutrality and the effect of stabilization presumably  
464 reflect a number of site-specific factors, including the degree to which stabilization causes a  
465 reduction in disturbance relative to the local regime. As maerl-associated species can recruit  
466 from other habitats, the composition of the areas adjacent to maerl beds may also cause local  
467 variation in the response to disturbance and stabilization.

468         This study of maerl communities is one of the first tests of Kadmon and Benjamini's  
469 (2006) hypothesis that species abundance and species richness responses to disturbance can be  
470 consistent with the DEM under a neutral model. The biomass and richness of algae increased at  
471 Zara and on tied maerl at Sketrick when wind speeds were low; however the details of species  
472 were unimportant, and species occurred at frequencies reflecting their abundance in the local  
473 pool. Similar neutral changes in animal species composition occurred on tied replicates at Zara.  
474 It might be expected that short exposures of tied replicates are quite likely to provide examples  
475 of neutral changes in species composition. Neutrality was not, however, confined to tied  
476 treatments, indicating that it may have a role in natural communities attached to maerl.

477         The non-neutral differences between tied and free treatments and with wind speeds for  
478 animals at Zara indicate the potential sensitivity of maerl-associated assemblages to changes in  
479 water motion. Different ecological traits appear to be favored under different conditions of  
480 mobility. Whether these different assemblages have fewer or more species varied between beds  
481 and between animals and algae.

482         Other than the broad-scale associations between environmental variables and the

483 associated biodiversity (Steller et al. 2003, Hinojosa-Arango and Riosmena-Rodriguez 2004),  
484 most information on maerl communities comes from anthropogenic impact studies (Hauton et  
485 al. 2003). The abundance of animals and algal biomass at Zara were dependent on the recent  
486 wind speeds. The influence of variable wind speeds was not so apparent at a site subject to  
487 relatively stronger tidal disturbances. Evidence for assemblages reflecting random sampling of  
488 the available pool (neutrality) and for some ecological structuring of assemblages was found.  
489 Whether neutral or due to ecological processes, the turnover of individuals between dates  
490 reflects an important role for migration into and out of the maerl habitat. The biodiversity of  
491 habitats such as maerl may therefore be particularly dependent on the nature and extent of  
492 adjacent habitats (Cole et al. 2007), requiring conservation measures to take the spatial context  
493 of beds into account.

494

#### 495 **Acknowledgments**

496 We thank C. Blake, A. Davies and S. Vize for their assistance in the field. G. Hinojosa-  
497 Arango is grateful to the Mexican Council for the Sciences and Technology (CONACYT) for a  
498 postgraduate scholarship.

499

500

#### **LITERATURE CITED**

501 Ansell, A. D. 1969. Leaping movements in the Bivalvia. Proceedings of the Malacological  
502 Society of London 38:387-399.

503 Basso, D. 1998. Deep rhodolith distribution in the Pontian Islands, Italy: a model for the  
504 paleoecology of a temperate sea. *Palaeogeography, Palaeoclimatology, Palaeoecology*.  
505 137:172-187.

506 Birkett, D. A., C. A. Maggs, and M. J. Dring. 1998. Maerl: an overview of dynamic and  
507 sensitivity characteristics for conservation management of marine SACs. Scottish  
508 Association of Marine Sciences, Dunstaffnage, UK.

- 509 Bosence, D. W. J. 1976. Ecological studies on two unattached coralline algae from western  
510 Ireland. *Paleontology* 19:365-395.
- 511 Bosence, D. W. J. 1985. The morphology and geology of a mound-building coralline alga  
512 (*Neogoniolithon structum*) from the Florida Keys. *Paleontology* 28:189-206.
- 513 Brown, R. 1990. Strangford Lough. The wildlife of an Irish Sea lough. PhD Thesis. Queen's  
514 University Belfast, Northern Ireland.
- 515 Bruno, J. F., and M. D. Bertness. 2001. Habitat modification and facilitation in benthic marine  
516 communities. In *Marine Community Ecology* (Bertness, M. D., Gaines, S.D. and Hay,  
517 M.E. eds). Sinauer Sunderland, MA.
- 518 Cabioch, J. 1969. Les fonds de maerl de la baie de Morlaix et leur peuplement végétal. *Cahiers*  
519 *de Biologie Marine* 10:139-161.
- 520 Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure.  
521 *Australian Journal of Ecology* 18:117-143.
- 522 Cole, V. J., M.G. Chapman, and A.J. Underwood. 2007. Landscapes and life-histories  
523 influence colonisation of polychaetes to intertidal biogenic habitats. *Journal of*  
524 *Experimental Marine Biology and Ecology* 348:191–199.
- 525 Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199:1302–1310.
- 526 Cutler, A. H. 1994. Nested biotas and biological conservation: metrics, mechanisms, and  
527 meaning of nestedness. *Landscape and Urban Planning* 28: 73-82.
- 528 Davies, A. J., and M. P. Johnson. 2006. Coastline configuration disrupts the effects of large-  
529 scale climatic forcing, leading to divergent temporal trends in wave exposure. *Estuarine,*  
530 *Coastal and Shelf Science* 69: 643-648.
- 531 Dayton, P. K. 1972. Toward an understanding of community resilience and the potential effects  
532 of enrichments to the benthos at McMurdo Sound, Antarctica. Pages 81–95 *in* B. C. Parker,  
533 editor. *Proceedings of the Colloquium on Conservation Problems in Antarctica*. Allen  
534 Press, Lawrence, Kansas, USA.

- 535 Ebeling, A.W., D. R. Laur, and R. J. Rowley. 1985. Severe storm disturbance and reversal of  
536 community structure in a southern California kelp forest. *Marine Biology* 84:287-294.
- 537 Foster, M. S. 2001. Mini-review: rhodoliths: between rocks and soft places. *Journal of*  
538 *Phycology* 37: 659-657.
- 539 Hall-Spencer, J. M., and P. G. Moore. 2000. Impact of scallop dredging on maerl grounds. In:  
540 Kaiser, M.J., De Groot, S.J. (Eds.), *The effects of fishing on non-target species and*  
541 *habitats*. Blackwell Science, San Diego, pp. 105-117.
- 542 Hall-Spencer, J. M., N. White, E. Gillespie, K. Gillham, and A. Foggo. 2006. Impact of fish  
543 farms on maerl beds in strongly tidal areas. *Marine Ecology Progress Series* 326:1-9.
- 544 Harris, P. T., Y. Tsuji, J. F. Marshall, P. J. Davies, N. Honda, and H. Matsuda. 1996. Sand and  
545 rhodolith-gravel entrainment on the mid- to outer-shelf under a western boundary current:  
546 Fraser Island continental shelf, eastern Australia. *Marine Geology* 129:313-330.
- 547 Hauton, C., J. M. Hall-Spencer, and P. G. Moore. 2003. An experimental study of the  
548 ecological impacts of hydraulic bivalve dredging on maerl. *Journal of Marine Science*  
549 60:381-392.
- 550 Higgins, C. L, M. R. Willig, and R. E. Strauss 2006. The role of stochastic processes in  
551 producing nested patterns of species distributions. *Oikos* 114: 159-167.
- 552 Hily, C., P. Potin, and Floch, J.Y. 1992. Structure of subtidal algal assemblages on soft-bottom  
553 sediments – fauna flora interactions and role of disturbances in the Bay of Brest, France.  
554 *Marine Ecology Progress Series* 85:115-130.
- 555 Hinojosa-Arango, G., and R. Riosmena-Rodríguez. 2004. Influence of rhodolith-forming  
556 species and growth-form on associated fauna of rhodolith beds in the Central-West Gulf of  
557 California, Mexico. *Proceedings of the Stazione Zoologica Napoli, Marine Ecology*  
558 25:109-127.
- 559 Hood, G. M. 2006. PopTools version 2.7.5. Available on the internet. URL  
560 <http://www.cse.csiro.au/poptools>

- 561 Hubbell, S. P. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*, Princeton  
562 University Press, Princeton, NJ.
- 563 Huston, M. A. 1979. A general hypothesis of species diversity. *American Naturalist* 113:81–  
564 101.
- 565 Johnson, M. P., N. J. Frost, M. W. J. Mosley, M. F. Roberts, and S. J. Hawkins. 2003. The  
566 area-independent effects of habitat complexity on biodiversity vary between regions.  
567 *Ecology Letters* 6:126-132.
- 568 Kadmon, R., and Y. Benjamini. 2006. Effects of productivity and disturbance on species  
569 richness: a neutral model. *American Naturalist* 167: 939–946.
- 570 Keegan, B. F. 1974. The macrofauna of maerl substrates on the west coast of Ireland. *Cahiers*  
571 *de Biologie* 15:513-530.
- 572 Kimbro, D. L., and E. D. Grosholz. 2006. Disturbance influences oyster community richness  
573 and evenness, but not diversity. *Ecology* 87: 2378–2388.
- 574 Koleff, P., K. J. Gaston, and J. J. Lennon. 2003. Measuring beta diversity for presence–absence  
575 data. *Journal of Animal Ecology* 72:367–382.
- 576 Kondoh, M. 2000. Unifying the relationships of species richness to productivity and  
577 disturbance. *Proceedings of the Royal Society of London Series B* 268: 269-271.
- 578 Littler, M. M., D. S. Littler, and M. D. Hanisak. 1991. Deep-water rhodolith distribution,  
579 productivity, and growth history at sites of formation and subsequent degradation. *Journal*  
580 *of Experimental Marine Biology and Ecology* 150:163-182.
- 581 Marrack, E. C. 1999. The relationship between water motion and living rhodolith beds in the  
582 southwestern Gulf of California, Mexico. *Palaios* 2:189-191.
- 583 Maughan, B. C., and D. K. A. Barnes. 2000. Epilithic boulder communities of Lough Hyne,  
584 Ireland: The influence of water movement and sediment. *Journal of the Marine Biological*  
585 *Association of the UK* 80: 767-776.
- 586 Menge, B. A., and J. P. Sutherland. 1976. Species diversity gradients: synthesis of the roles of

- 587 predation, competition, and temporal heterogeneity. *American Naturalist* 110:351-369.
- 588 Patterson, B. D., and W. Atmar. 1986. nested subsets and the structure of insular mammalian  
589 faunas and archipelagoes. *Biological Journal of the Linnean Society* 28: 65-82.
- 590 Petraitis, P. S., R. E. Latham, and R. A. Niesenbaum. 1989. The maintenance of species  
591 diversity by disturbance. *Quarterly Review of Biology* 64:393-418.
- 592 Petren, K., and T. J. Case. 1998. Habitat structure determines competition intensity and  
593 invasion success in gecko lizards. *Proceedings of the National Academy of th USA*  
594 95:11739-11744.
- 595 Quinn, G. P., and M. J. Keough. 2002. *Experimental Design and Data Analysis for Biologists*.  
596 Cambridge University Press, Cambridge, UK.
- 597 Steller, D. L., and M. S. Foster. 1995. Environmental factors influencing distribution and  
598 morphology of rhodoliths in Bahia Concepcion, B.C.S., Mexico. *Journal of Experimental*  
599 *Marine Biology and Ecology* 194:201-212.
- 600 Steller, D. L., R. Riosmena-Rodríguez, R., Foster, M. S., and C.A. Roberts. 2003. Rhodolith  
601 bed diversity in the Gulf of California: the importance of rhodolith structure and  
602 consequences of disturbance. *Aquatic Conservation: Marine and Freshwater Ecosystems*  
603 13:S5–S20.
- 604 Steneck, R. S. 1986. The ecology of coralline algal crusts: convergent patterns and adaptative  
605 strategies. *Annual Review of Ecology and Systematics* 17:273-303.
- 606 Ulrich, W., and N. J. Gotelli 2007. Null model analysis of species nestedness patterns. *Ecology*  
607 88: 1824–1831.
- 608

609 Table 1. Analysis of covariance for the effect of wind speed and stabilization on the abundance and biomass of maerl associated species.  
 610 Homogeneity of slopes between treatments was tested using a full ANCOVA model that included a stabilization treatment x wind speed  
 611 interaction. This term was subsequently removed from fitted models except for the one case where it was significant. The null hypotheses of  
 612 homogeneous slopes were therefore accepted for all cases except algal biomass at Sketrick. Degrees of freedom for the residual in the model with  
 613 an interaction term were 68. Main effects F ratios are not shown for the model with an interaction as they are difficult to interpret in this case.

Bed	Species group	MS wind speed (df 1)	MS stabilization (df 1)	MS interaction (df 1)	MS residual (df 69, 168)	F <sub>1,69</sub> wind	F <sub>1,69</sub> stabilization	F <sub>1,68</sub> interaction
Sketrick	sessile	0.001	5.774	-	0.367	0.00	15.72***	-
Sketrick	mobile	0.497	1.045	-	0.153	3.26	6.85*	-
Sketrick	algae	1.074	3.583	2.912	0.357	-	-	8.15**
Zara	sessile	1.200	0.152	-	0.130	9.20**	1.16	-
Zara	mobile	1.580	0.681	-	0.136	11.66**	5.02*	-
Zara	algae	2.642	0.118	-	0.150	17.60***	0.79	-

614

615

616 Table 2. Covariance of species richness with wind speed and stabilization treatment. Homogeneity of slopes between treatments was tested using  
 617 a full ANCOVA model that included a stabilization treatment x wind speed interaction. This term was not significant for any of the analyses.  
 618 The null hypotheses of homogeneous slopes were therefore accepted and the interaction was omitted from the final models.

619

Bed	Species group	MS wind speed (df 1)	MS stabilization (df 1)	MS residual (df 69)	F <sub>1,69</sub> wind	F <sub>1,69</sub> stabilization
Sketrick	sessile	5.318	2.000	3.604	1.48	0.55
Sketrick	mobile	8.020	117.56	15.750	0.51	7.46**
Sketrick	algae	74.769	32.000	3.170	23.59***	10.09**
Zara	sessile	17.639	117.347	7.831	2.25	22.65***
Zara	mobile	146.730	117.350	38.670	3.79	4.59*
Zara	algae	45.802	34.722	5.064	9.04**	6.86*

620

621 Table 3. Non parametric correlations between wind speed matrix and similarity matrices. The  
 622 null association between matrices was estimated by randomly selecting individuals from an  
 623 abundance distribution based on all samples within a treatment. For details of methods see text.  
 624 Confidence intervals are the result of 499 random selections. As the test is for a neutral response  
 625 to wind-related disturbance, results are presented only where wind speed had a significant effect  
 626 on abundance or biomass. Observed correlations between matrices that lie outside the expected  
 627 values for a neutral assemblage are highlighted in bold.  
 628

Bed	Species group	Treatment	Observed $r_s$	Null $r_s$	95 % confidence intervals
Sketrick	algae	tied	0.262	0.180	0.049 to 0.294
Zara	sessile	tied	-0.123	-0.132	-0.203 to -0.052
Zara	sessile	free	<b>-0.009</b>	-0.156	-0.217 to -0.086
Zara	mobile	tied	0.239	0.230	0.149 to 0.312
Zara	mobile	free	<b>-0.005</b>	-0.069	-0.124 to -0.009
Zara	algae	tied	0.124	0.053	-0.075 to 0.255
Zara	algae	free	-0.059	0.048	-0.089 to 0.189

629 Table 4. Randomization tests for the hypothesis that tied and free assemblages are samples from  
 630 the same underlying species abundance distribution. Differences between assemblages are  
 631 measured with the ANOSIM test statistic (R). Null values generated by sampling from the same  
 632 species abundance distribution for each treatment. Observed R values falling outside the  
 633 expected range are highlighted in bold.  
 634

Bed	Species group	Observed R	Null R	95 % confidence intervals
Sketrick	sessile	<b>0.275</b>	0.074	0.027 to 0.136
Sketrick	mobile	<b>0.459</b>	0.024	-0.011 to 0.050
Sketrick	algae	<b>0.087</b>	0.009	-0.018 to 0.042
Zara	Sessile	<b>0.509</b>	-0.003	-0.029 to 0.028
Zara	mobile	<b>0.399</b>	0.011	-0.007 to 0.032
Zara	algae	<b>0.137</b>	0.011	-0.015 to 0.037

635

636 **Figure legends**

637 Fig. 1. Wind speed records from Belfast Harbor, c. 30 km from Strangford Lough. Averages  
638 represent the two month period ending in the month shown. The line of numbers refers to the  
639 number of days with an average wind speed exceeding  $6 \text{ m s}^{-1}$  in the two month period. Error  
640 bars are SE.

641

642 Fig. 2. Relationships between wind speeds and abundance of animals or biomass of algae at the  
643 different beds. Lines are significant fitted ANCOVA slopes unless the effect of wind speed was  
644 not significant, in which case the line is the mean of the data. Panels are divided into sessile  
645 animals (a, b), mobile animals (c, d) and algae (e, f) at the different beds (Sketrick and Zara).  
646 Treatments are shown with filled symbols and solid lines for tied maerl, open symbols and  
647 dotted lines for free maerl. Dashed lines indicate no significant difference between tied and free  
648 treatments.

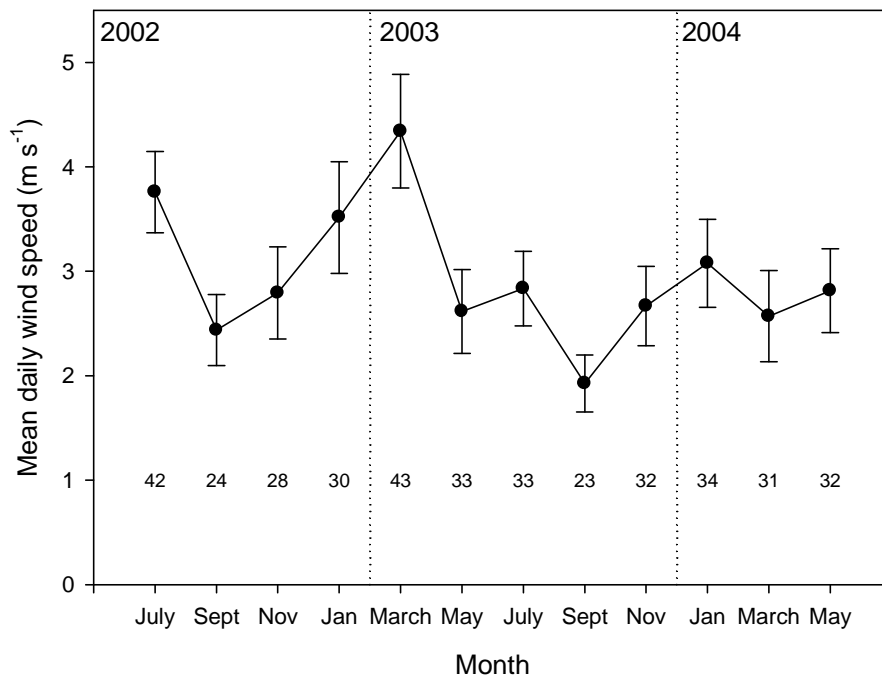
649

650 Fig. 3. Effect of wind speed and stabilization on species richness of sessile animals (a, b),  
651 mobile animals (c, d) and algae (e, f) at the different beds (Sketrick and Zara). Tied treatments  
652 are indicated with solid lines and filled symbols with dotted lines and open symbols for free  
653 maerl. Slopes are drawn where the effect of wind speed was significant in ANCOVA. In the  
654 absence of a significant effect of the covariate the means of treatments are indicated, unless  
655 these means were not significantly different (overall mean: dashed line).

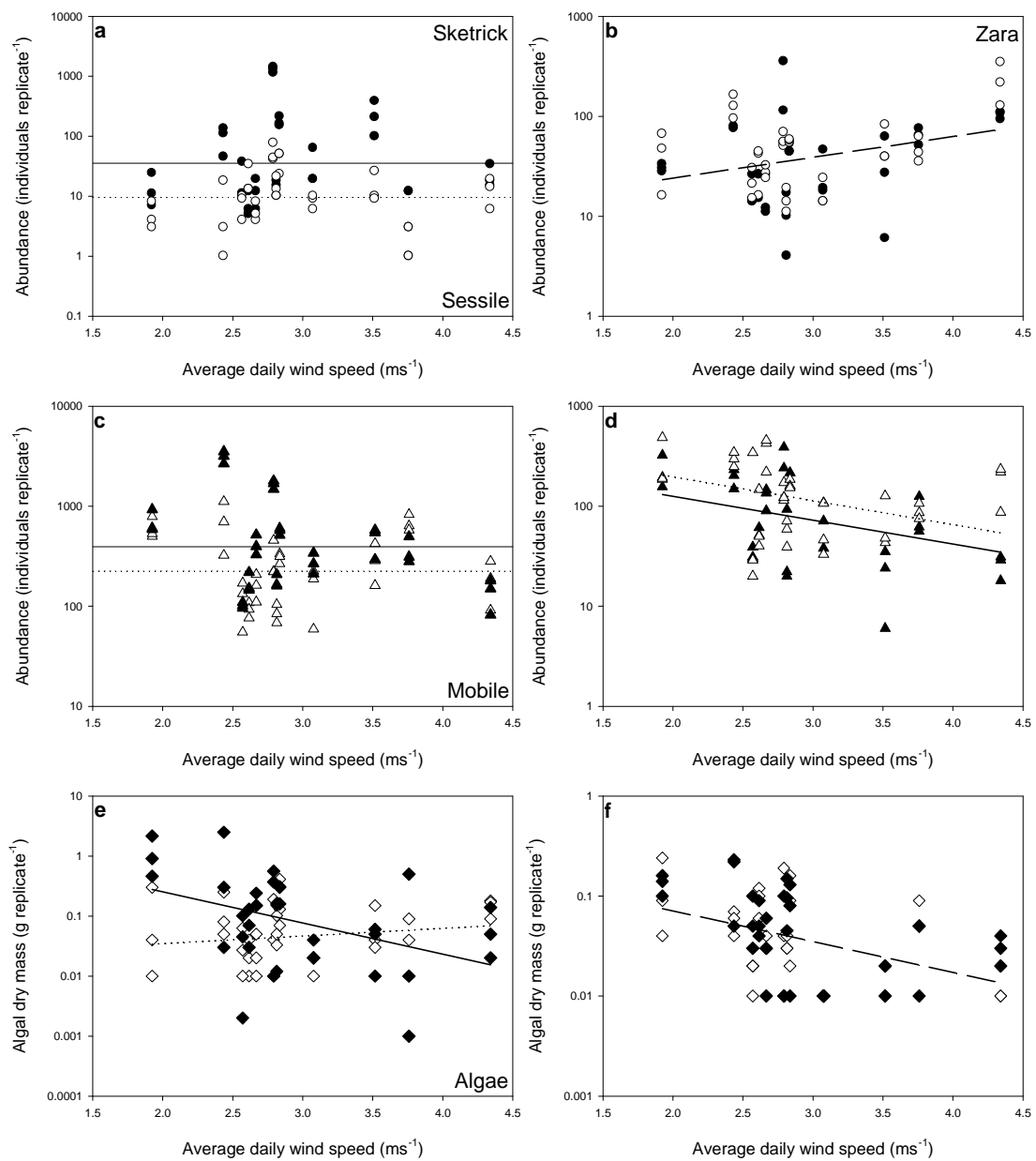
656 Fig. 1.

657

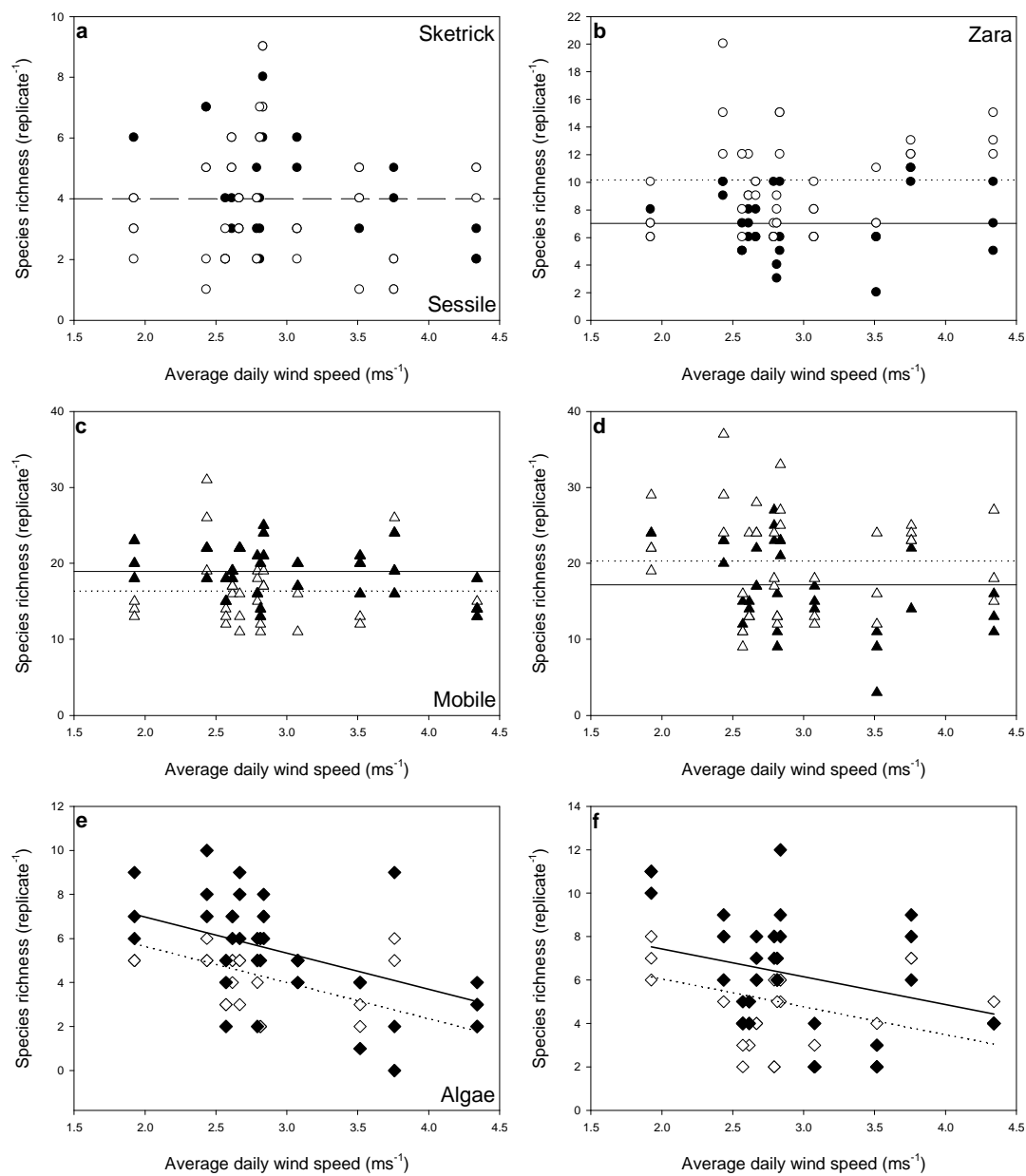
658



659 Fig. 2.



661 Fig. 3.



662