

# Like a rolling stone: the mobility of maerl (Corallinaceae) and the neutrality of the associated assemblages

GUSTAVO HINOJOSA-ARANGO,<sup>1</sup> CHRISTINE A. MAGGS, AND MARK P. JOHNSON<sup>2</sup>

*School of Biological Sciences, Queen's University Belfast, 97 Lisburn Road, Belfast, Northern Ireland BT9 7BL*

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

*Key words:* coralline algae; disturbance; maerl beds; nestedness; *Phymatolithon calcareum*; rhodolith; stability; Strangford Lough, Northern Ireland.

## INTRODUCTION

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

It is possible that the natural patterns of disturbance in maerl beds affect the associated biodiversity (more is known about the effects of anthropogenic disturbances; Hall-Spencer and Moore 2000, Hauton et al. 2003, Hall-Spencer et al. 2006). In the context of community ecology, disturbance is often linked to patterns of species diversity. A well-known case is the intermediate disturbance hypothesis (IDH; Connell 1978), which proposes a unimodal relationship between disturbance and diversity with the highest species richness under intermediate disturbance. A related theory is Huston's (1979) dynamic equilibrium model (DEM; see also Kondoh 2000), which modifies the relationship between disturbance and diversity according to productivity. For example, under low productivity diversity decreases monotonically with disturbance as the resource-limited conditions under which competitive displacement occurs are never reached. Most theoretical explanations for the IDH and DEM are based on trade-offs between the ecological traits of species, generally invoking a competitive hierarchy (Petraitis et al. 1989, Kondoh 2000). There are two contrasting alternatives to the idea that

Manuscript received 21 December 2007; revised 6 May 2008; accepted 2 June 2008. Corresponding Editor: R. B. Aronson.

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

<sup>2</sup> Present address: Martin Ryan Institute, National University of Ireland, Galway, University Road, Galway, Ireland. E-mail: mark.p.johnson@nuigalway.ie

competitive interactions underlie disturbance–diversity relationships. A simulation model is used by Kadmon and Benjamini (2006) to demonstrate that neutral theory can produce disturbance–diversity relationships without invoking differences in ecological traits among species. A non-neutral alternative is that facilitation by foundation species may override competitive exclusion (Bruno and Bertness 2001). The mechanism for this facilitation effect relates to the situation in which a foundation species constructs a more complex habitat under conditions of low disturbance. Greater habitat complexity can lead to a greater surface area and a greater level of heterogeneity (Johnson et al. 2003). Greater surface area and heterogeneity can dilute the strength of competitive interactions (Petren and Case 1998), causing species diversity to monotonically increase as disturbance decreases. The aim of the current study was therefore to evaluate negative, neutral, and positive interactions in the response of maerl-associated species to the natural range of disturbance.

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

At small spatial scales, the assemblages on maerl beds are likely to be open: recruits will come from a wide area rather than through local reproduction. The composition of the regional species pool (metacommunity; Hubbell 2001) in immigration-dominated assemblages such as this can be estimated from the average species abundance distribution across all samples. Hubbell's neutral theory therefore emphasizes the relative abundances of species in addition to the accumulated inventory at the scale in question. In a neutral assemblage, differences in species composition along a gradient of disturbance should be no greater than the

differences in composition between random samples from the regional species pool (Kadmon and Benjamini 2006). The appeal of neutral theories is that tractable generalizations may be possible without the need for detailed species-specific information. In contrast, the IDH and DEM models emphasize the importance of species traits: species are more likely to be found at particular disturbance frequencies due to being, for example, competitive dominants or superior colonists. Hence under IDH and DEM, species assemblages at different levels of disturbance are likely to be more dissimilar than expected when compared to a random selection from the regional pool.

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

The three-dimensional matrix of a maerl bed is probably a greater resource for animals than it is for algae, which depend on light falling on the upper surface of the bed. This may result in algae having a lower net benefit from stabilization of maerl and a higher likelihood of interspecific competition. In addition, many maerl-associated species are found in adjacent habitats (Birkett et al. 1998). This may lead to mobile animals moving in and out of the maerl matrix with changing disturbance. Data from the current study were therefore analyzed separately for mobile animals, sessile animals, and algae to test whether neutral responses to disturbance were more common in the assemblage of mobile animals.

## METHODS

### *Study system*

Maerl beds occur from the lowermost intertidal zone to depths of over 100 m (Littler et al. 1991). The ecological importance of maerl habitats is recognized by, for example, listing of maerl species in the European Union's Habitats Directive (92/43/EEC). Maerl beds are reported to support richer communities than habitats of equivalent grain size such as gravel or shell bottoms (Cabioch 1969, Keegan 1974). Causes of the relatively high species diversity in maerl beds are unclear (Foster

2001). The three-dimensional structure of maerl beds is likely to increase surface area and habitat diversity, both of which may facilitate greater species coexistence.

Hydrodynamics play a key role in the distribution, shape, branching pattern, and stability of maerl thalli (Bosence 1976, 1985, Steneck 1986, Hily et al. 1992, Steller and Foster 1995, Basso 1998). Maerl beds do not develop if water movement is so slight that beds are covered by sediment or where water movement is too high, leading to destruction or unsustainable loss rates of thalli (Foster 2001). In between these extremes of water movement, periodic rotation is necessary for maerl as it allows light to reach all sides of the thalli and retards burial and fouling (Steneck 1986). Such periodic rotation represents a potential disturbance event to species associated with maerl. During turnover events, attached flora and fauna could be abraded or buried on the underside of maerl thalli and motile fauna impacted by abrasion between thalli. Such disturbances are frequently seen as preventing the development of a stable community (Menge and Sutherland 1976, Ebeling et al. 1985, Maughan and Barnes 2000). A further effect of thallus movement is that the habitat may become less structurally complex due to breakage of more complex thalli and the loss of habitat heterogeneity as, on average, more thalli experience the same conditions as opposed to persistent differentiation between surface and buried thalli.

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

As the studied beds are relatively shallow, they are susceptible to disturbance from wind-generated waves. The shelter at Sketrick prevents much wave activity, but

Zara is more affected by wind-driven waves. In the study by Davies and Johnson (2006), shores adjacent to the Sketrick bed were in the most sheltered quartile of sites around the shores of Strangford Lough, while the shores closest to Zara were in the most exposed quartile of sites. Marrack (1999) estimated that wind speeds in excess of 6 m/s for periods >4 h would move thalli at depths of 4–5 m in the Isla el Requesón bed off Baja California. Average daily wind speeds in Strangford are generally greater than those at the Isla el Requesón. On average there were 16 days each month at Strangford with a wind speed exceeding 6 m/s during the period when experiments were carried out (Fig. 1). Such frequencies are comparable to the winter month data in Marrack (1999), in which movement of thalli was observed to be “frequent.” At the scale at which experiments were carried out, there was no evidence for seasonality in wind speeds at Strangford. For example, the highest average daily wind speed was observed in March 2003, but March 2004 had one of the lowest mean wind speeds. Average daily wind speed and frequency of days with average speeds >6 m/s were highly correlated ( $r = 0.853$ ,  $P < 0.001$ ). There was no pattern of autocorrelation in the wind time series. The autocorrelation at a two-month lag was 0.067 and the Ljung-Box  $Q$  statistic for lags up to 6 was 7.663 (not significant against  $\chi^2$  distribution, df 6, no significant lags). Tidal currents can also move maerl thalli, but the variation among separate two-month experimental periods at Strangford was low (coefficient of variation for maximum tidal range 7%). Tides are likely to represent a continual background amount of thallus movement with little variation over time.

#### *Experimental treatments*

Maerl were artificially stabilized at the two beds in Strangford Lough to examine the effects of reduced mobility on the assemblage of associated species. Many variables are likely to vary between the live and dead maerl beds. Such factors confound a simple comparison of the two beds; therefore the experimental design does not formally compare the beds, and the main analyses presented (on neutrality) are not dependent upon a comparison between beds. Variation in mean daily wind speed was used as a covariate to test for changes in community structure associated with disturbance. Increasing wind speeds were predicted to cause lower species diversities and abundances due to the disturbance of thallus movement. If competitive interactions and trade-offs are important, then species were expected to be added nonrandomly to treatments as wind speed decreased. Higher abundances of animals and biomass of algae were predicted for stabilized treatments. If competitive exclusion becomes important within the scales investigated, then evidence for a unimodal relationship between diversity and disturbance or a lowered species diversity in stabilized vs. free replicates was predicted (IDH).

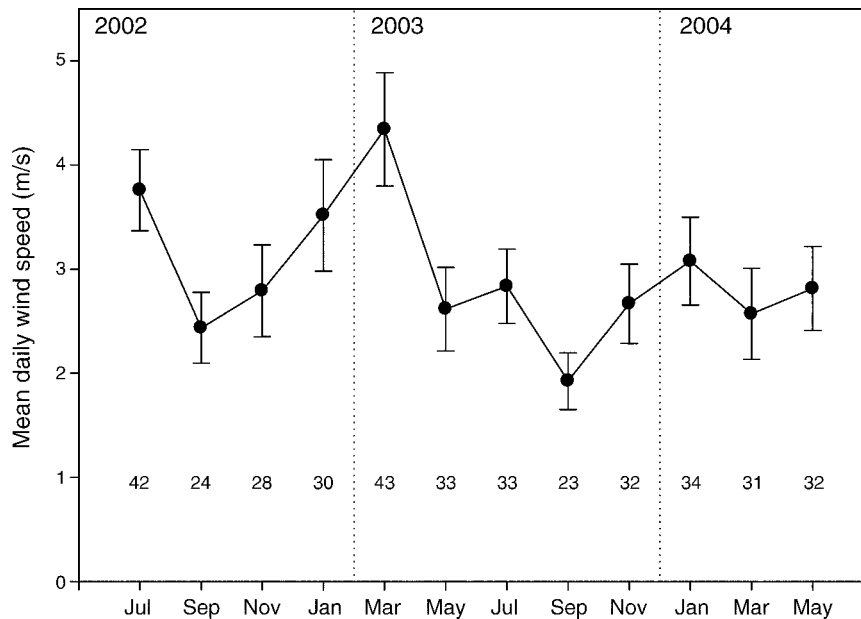


FIG. 1. Wind speed records (mean  $\pm$  SE) from Belfast Harbor,  $\sim$ 30 km from Strangford Lough, Northern Ireland. Means represent the two-month period ending in the month shown. Numbers in panels refer to the number of days with an average wind speed exceeding 6 m/s in the two-month period.

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

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

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

Species associated with stabilized maerl were compared to specimens collected from three quadrats of natural, free-moving maerl. These samples were collected by placing a plastic cage  $15 \times 15 \times 4$  cm haphazardly over the maerl bed, in the same area in which concrete blocks had been placed. The underside of the cage was sealed by sliding a plastic sheet underneath, with enclosed material transferred carefully to labeled plastic bags. Replicates of "free" maerl were therefore of the same dimensions and thickness as stabilized treatments. A total of 12 sampling dates resulted in the collection of 72 samples at each maerl bed (36 artificially stabilized maerl and 36 free maerl quadrats).

#### Sample processing

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

Following removal of algal material, samples were fixed in 4% formalin-seawater and preserved in a 70% alcohol solution. Sessile organisms such as ascidians, sponges, and some molluscs were removed using forceps. Samples were shaken to remove vagile organisms, with the alcohol solution from each sample sieved through a 0.5-mm mesh to collect fauna. The retained sediment was sorted under a binocular dissecting microscope to extract any remaining organisms. Epi-

fauna were identified to species, genus, or to the best resolution possible. Due to the difficulties in recognizing individuals of encrusting colonial invertebrates, these groups were counted as one individual for each maerl piece to which they were attached. Counts for these species may therefore underrepresent the number of separate colonization events.

#### *Statistical analyses*

Species richness was calculated for each replicate for both algae and animals. Due to difficulties in unambiguously identifying individual algae and the wide variation in thallus sizes, total abundance of individuals was only calculated on the basis of counted animal species. The equivalent variable for algae was total dry mass of attached fronds. All response variables were compared between stabilized (tied) and free maerl treatments using ANCOVA, with average daily wind speed during the relevant two-month exposure period as the covariate. Homogeneity of slopes was assessed for each treatment against wind speed ANCOVA by fitting a full model that included the treatment  $\times$  wind speed interaction. A significant interaction implies that the rate of change in a response variable with respect to wind speeds differs between treatments: the slopes are heterogeneous. In this case results are presented using the separate slopes for each treatment. Where the interaction was not significant, homogeneity of slopes was assumed, and results are presented from a simple (no interaction fitted) ANCOVA model with parallel slopes in the different treatments (Quinn and Keough 2002). Results from the simple model are presented as two parallel lines or a single line, depending upon the significance of the treatment effect. Nonsignificant results for the covariate are presented without a slope; just the mean for each treatment is used. Assumptions of linearity and heterogeneity of variances were examined using residual plots. There was no evidence of the systematic deviation from random scatter that might be associated with nonlinearity or heteroscedasticity in the data for species richness. Algal biomass and animal abundances required logarithmic transformation to produce acceptable patterns in the residuals.

Changes in the overall structure of assemblages were evaluated with multivariate techniques. Systematic variation in assemblage structure with changing wind speeds was assessed by calculating the nonparametric correlation between a similarity matrix based on multivariate distances between the replicates (Sørensen coefficient) and a similarity matrix between dates based on mean wind speed. Positive correlations between wind and species-based distance matrices imply that periods of different wind speed have different assemblages. Such differences could be due to species' responses to disturbance and patterns arising from other ecological traits such as competitive ability. However, a correlation between distance matrices could be produced simply by changes in abundance among replicates. This occurs as

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

The neutral model as tested here has some similarities with tests of “nestedness” (Patterson and Atmar 1986). When communities are nested, the compositions of less rich communities form subsets of richer communities. A neutral model will form this pattern as the relatively abundant species will be in most samples while rarer species will only occur in communities with high numbers of individuals or biomass. This mechanism is recognized in the nestedness literature as “passive sampling” (Cutler 1994, Higgins et al. 2006, Ulrich and Gotelli 2007). The nestedness literature has frequently used null models to test for nestedness that rely on stochastic placement of species rather than individuals (Higgins et al. 2006). This means that the available software is not generally suitable for tests of a neutral model. A second distinction between the approach in the current study and the nestedness literature is that calculations of nestedness generally rank samples by species richness. The tests of disturbance presented here make a more explicit hypothesis by testing for nested structure along a proposed gradient of disturbance (wind stress). The neutral model tested in this study is therefore a more explicit hypothesis than existing tests of nestedness. Measurements of nestedness should, however, be consistent with our analyses. Matrix “temperatures” were therefore calculated for all taxon matrices using the methods in Ulrich and Gotelli (2007), in which progressively stronger nesting results in a lower

TABLE 1. ANCOVA for the effect of wind speed and stabilization on the abundance and biomass of maerl-associated species at two sites in Strangford Lough, Northern Ireland.

Species group, by site	MS wind speed	MS stabilization	MS interaction	MS residual	$F_{1,69}$ wind	$F_{1,69}$ stabilization	$F_{1,68}$ interaction
Sketrick							
Sessile	0.001	5.774	...	0.367	0.00	15.72***	...
Mobile	0.497	1.045	...	0.153	3.26	6.85*	...
Algae	1.074	3.583	2.912	0.357	...	...	8.15**
Zara							
Sessile	1.200	0.152	...	0.130	9.20**	1.16	...
Mobile	1.580	0.681	...	0.136	11.66**	5.02*	...
Algae	2.642	0.118	...	0.150	17.60***	0.79	...

Notes: Homogeneity of slopes between treatments was tested using a full ANCOVA model that included a stabilization treatment  $\times$  wind speed interaction. This term was subsequently removed from fitted models except for the one case in which it was significant. Ellipses mean no interaction test result is presented as the final model did not calculate the related MS estimate or  $F$  value. The null hypotheses of homogeneous slopes were therefore accepted for all cases except algal biomass at Sketrick. Degrees of freedom for the residual in the model with an interaction term were 68. Main-effects  $F$  ratios are not shown for the model with an interaction because they are difficult to interpret in this case.

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

matrix temperature. The matrix temperature is an analogy to thermodynamics, but as a ratio it does not have units of measurement.

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

## RESULTS

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

treatments at Zara had 86 animal species and 20 algae in common.

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

### Effects of maerl mobility on assemblages

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

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

Cases in which wind speed appeared to be affecting the abundance or biomass of assemblages were examined for evidence of non-neutral changes in assemblages. In most cases the measured association between species-based distance matrices and the wind speed–distance matrix were within the confidence limits of a neutral

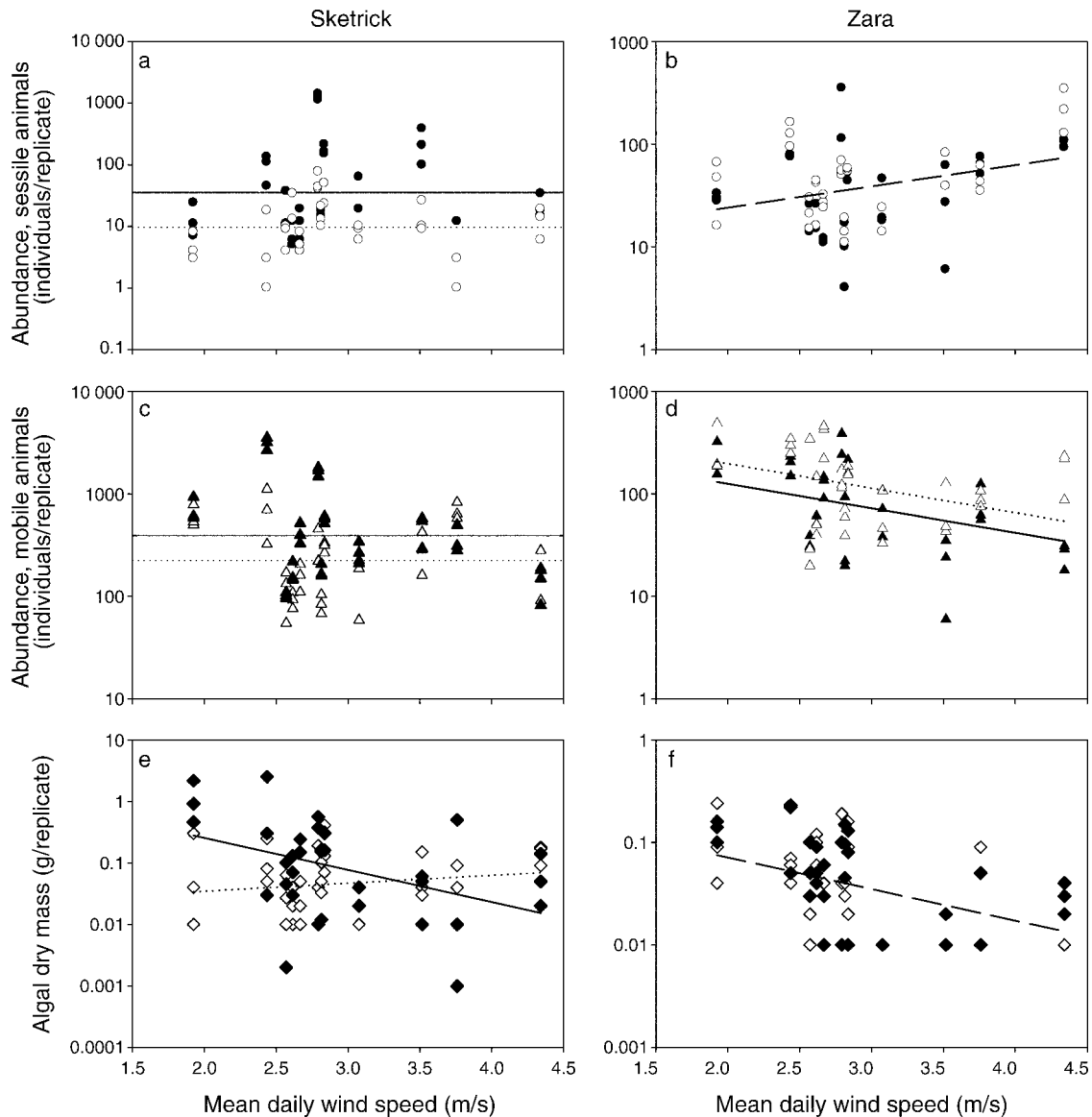


FIG. 2. Relationships between wind speed and abundance of animals or biomass of algae (note y-axis log scales) at the different beds. Lines are significant fitted ANCOVA slopes unless the effect of wind speed was not significant, in which case the line is the mean of the data. Panels are divided into (a, b) sessile animals, (c, d) mobile animals, and (e, f) algae at the different beds (Sketrick and Zara). Tied-maerl (artificially stabilized) treatments are indicated with solid symbols and solid lines; free-maerl treatments are indicated with open symbols and dotted lines. Dashed lines in panels (b) and (f) indicate no significant difference (at  $P < 0.05$ ) between tied and free treatments.

model. Changes in assemblages were no more structured than would be expected with random selection of species from the available pool (Table 3). Free maerl treatments at Zara were an exception to this pattern. The association between wind speed and assemblage matrices in these cases was higher than the upper confidence interval. There was greater discrimination between assemblages at different wind speeds than might be expected from neutrality.

Calculated matrix temperatures were consistent with the results from the more explicit test for association

with wind speed. The two treatments that significantly departed from a neutral response to wind disturbance had the lowest degree of nesting (temperatures greater than 18). As would be expected under passive sampling, experimental treatments that conformed to a neutral model had lower matrix temperatures (range 5–13).

*Differences among experimental treatments*

Stabilizing maerl always increased algal species richness with respect to free maerl. The results for animals are more mixed (Table 2). Both mobile and

TABLE 2. Covariance of species richness with wind speed and stabilization treatment.

Species group, by site	MS wind speed	MS stabilization	MS residual	$F_{1,69}$ wind	$F_{1,69}$ stabilization
Sketrick					
Sessile	5.318	2.000	3.604	1.48	0.55
Mobile	8.020	117.56	15.750	0.51	7.46**
Algae	74.769	32.000	3.170	23.59***	10.09**
Zara					
Sessile	17.639	117.347	7.831	2.25	22.65***
Mobile	146.730	117.350	38.670	3.79	4.59*
Algae	45.802	34.722	5.064	9.04**	6.86*

Notes: Homogeneity of slopes between treatments was tested using a full ANCOVA model that included a stabilization treatment  $\times$  wind speed interaction. This term was not significant for any of the analyses. The null hypotheses of homogeneous slopes were therefore accepted, and the interaction was omitted from the final models.

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

sessile animal groups were less species-rich on stabilized maerl than on free maerl at Zara. Tying maerl down resulted in the opposite effect with mobile animal species at Sketrick and no difference in richness among treatments for sessile species at this site.

The assemblages on tied and free maerl differed more than would be expected under a neutral model. The dissimilarities between treatments were not solely due to sampling different numbers of individuals from a common species pool (Table 4). The hypothesis of neutrality between treatments could therefore be rejected with species-specific ecology invoked to explain the different assemblages found on tied and free maerl.

## DISCUSSION

### *Neutrality and responses to disturbance*

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

The neutral model was not, however, universally applicable to results. Disturbance by higher winds was associated with lower abundances of mobile animals on free maerl at Zara. Species assemblages on free maerl at Zara were, however, more distinct at different wind speeds than would be expected from random sampling

of the same species pool. Under a neutral model, all mobile species would be expected to have negative correlations with wind speed as overall abundance also decreases under windier conditions. The most extreme departures from this pattern were species either insensitive to wind speed or showing slight increases in abundance with wind speed. For example, *Hydrobia neglecta*, *Achelia longipes*, and *Ophiura albida* all had correlations with wind speed exceeding 0.24. The rejection of neutrality suggests that these species are more likely to colonize maerl under windier conditions or they may be excluded by ecological interactions at low wind speeds. The same species were more common in free maerl than in stabilized treatments, which is consistent with some preference for a more mobile substratum.

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

### *Disturbance–diversity relationships*

The relationships between disturbance and species richness were varied. Only algal species richness was associated with variation in wind speed. This pattern was consistent with the neutral interactions leading to the pattern predicted under the DEM with low productivity (increased biomass and species richness



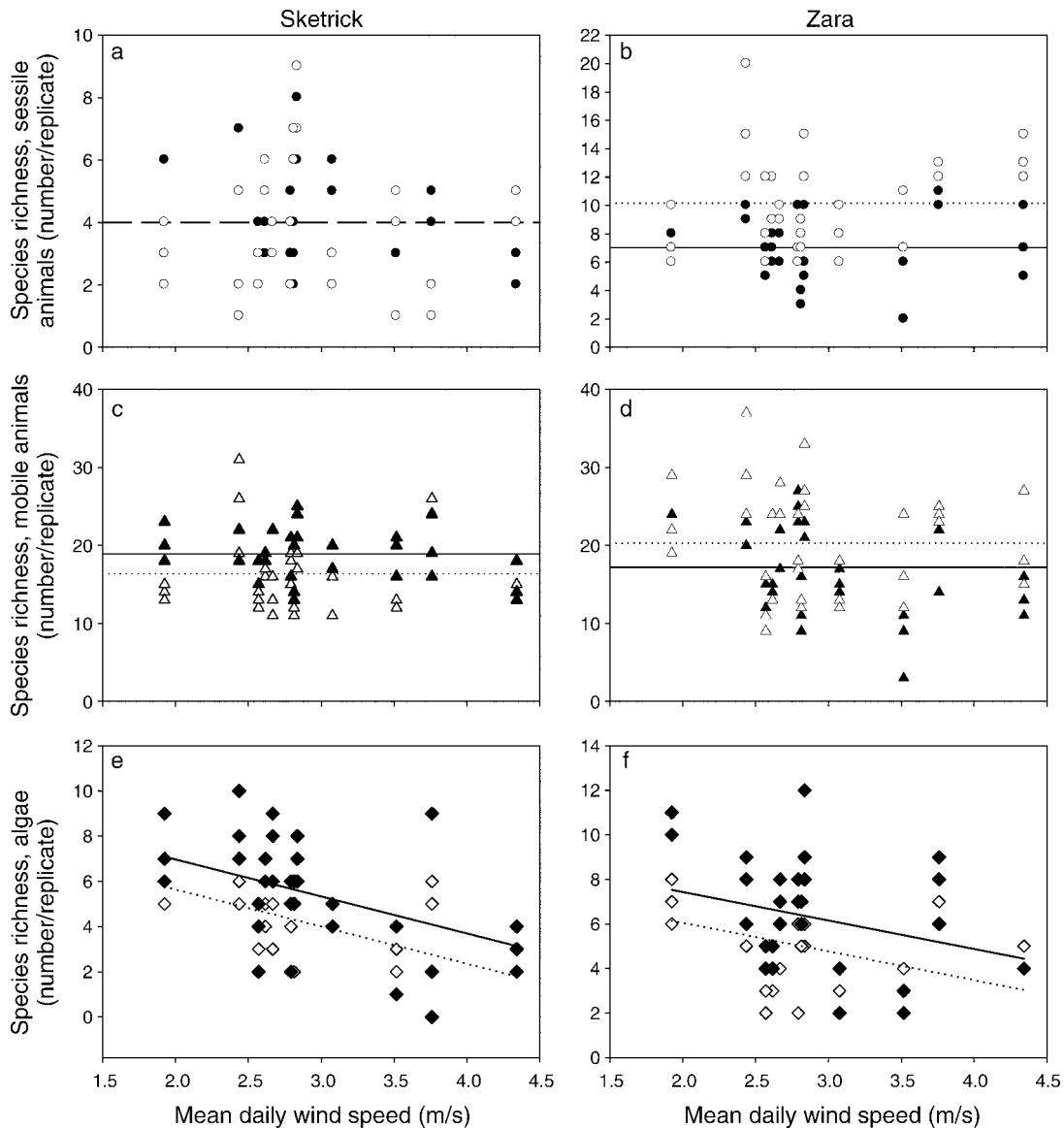


FIG. 3. Effect of wind speed and stabilization on species richness of (a, b) sessile animals, (c, d) mobile animals, and (e, f) algae at the different beds (Sketrick and Zara). Tied-maerl (stabilized) treatments are indicated with solid lines and solid symbol; free-maerl treatments are indicated with dotted lines and open symbols. Slopes are drawn in cases in which the effect of wind speed was significant in ANCOVA (at  $P < 0.05$ ). In the absence of a significant effect of the covariate, the means of treatments are indicated, unless these means were not significantly different; the overall mean is indicated by the dashed line in panel (a).

under low disturbance). Within the timescale of the experiment there was no evidence for a reduction in algal species richness under low disturbance. Either the biomass at which competitive exclusion is important is not reached, even on stabilized maerl, or there are facilitation effects that offset any competitive exclusions (Bruno and Bertness 2001). Variable wind speeds had no effect on mobile or sessile animal species richness. Stabilization was proposed to cause a reduction in disturbance and an opportunity for the number of individuals and species to increase relative to free maerl. Richness in stabilized maerl was, however, found to be

equal to, lower, or higher than on free maerl, depending on species' mobility and site. Results from Zara suggest that increasing stability of maerl will result in lower species numbers. This may be due to lower numbers of individuals (mobile species) or due to other changes in the assemblage, potentially including competitive interactions (sessile species). Similarly, the pattern for mobile species richness at Sketrick follows the increased abundance of individuals on stabilized maerl. Associations between the relative abundances and species richness counts between treatments are consistent with the facilitation hypothesis or the DEM. The IDH was

TABLE 3. Nonparametric correlations between wind speed matrix and similarity matrices.

Species group, by site	Treatment	Observed $r_S$	Null $r_S$	95% CI
Sketrick				
Algae	tied	0.262	0.180	0.049 to 0.294
Zara				
Sessile	tied	-0.123	-0.132	-0.203 to -0.052
Sessile	free	<b>-0.009</b>	-0.156	-0.217 to -0.086
Mobile	tied	0.239	0.230	0.149 to 0.312
Mobile	free	<b>-0.005</b>	-0.069	-0.124 to -0.009
Algae	tied	0.124	0.053	-0.075 to 0.255
Algae	free	-0.059	0.048	-0.089 to 0.189

*Notes:* The null association between matrices was estimated by randomly selecting individuals from an abundance distribution based on all samples within a treatment: artificially tied maerl beds (stabilized) vs. free maerl beds. Confidence intervals are the result of 499 random selections. As the test is for a neutral response to wind-related disturbance, results are presented only in cases in which wind speed had a significant effect on abundance or biomass (at  $P < 0.05$ ). Observed correlations between matrices that lie outside the expected values for a neutral assemblage appear in boldface.

generally not supported, at least over the timescales of experiments. It may be that competitive dominants can only depress species numbers over longer timescales.

#### *Differences between sites and treatments*

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

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

The presence of adult molluscs and crustaceans in stabilized maerl indicates that migration of mobile fauna is common. Migrations of sessile fauna are also possible. The category of "sessile" in this study included bivalves, and this group numerically dominated counts of sessile species ( $90.3\% \pm 1.04\%$  [mean  $\pm$  SE] of all counted individuals). Bivalves, while not as mobile as crustaceans, are not permanently attached (Ansell 1969). The response of sessile animals (increase in abundance at Zara) to increased wind speeds may indicate immigration from more disturbed environments into maerl. Alternatively, maerl may not be a favored habitat when disturbance is low, perhaps due to siltation.

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

This study of maerl communities is one of the first tests of Kadmon and Benjamini's (2006) hypothesis that species abundance and species richness responses to disturbance can be consistent with the DEM under a neutral model. The biomass and richness of algae increased at Zara and on tied maerl at Sketrick when wind speeds were low; however, the details of species were unimportant, and species occurred at frequencies reflecting their abundance in the local pool. Similar neutral changes in animal species composition occurred on tied replicates at Zara. It might be expected that short exposures of tied replicates are quite likely to provide

TABLE 4. Randomization tests for the hypothesis that tied and free maerl assemblages are samples from the same underlying species abundance distribution.

Species group, by site	Observed $R$	Null $R$	95% CI
Sketrick			
Sessile	<b>0.275</b>	0.074	0.027 to 0.136
Mobile	<b>0.459</b>	0.024	-0.011 to 0.050
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
Mobile	<b>0.399</b>	0.011	-0.007 to 0.032
Algae	<b>0.137</b>	0.011	-0.015 to 0.037

*Notes:* Differences between assemblages are measured with the ANOSIM test statistic ( $R$ ). Null values were generated by sampling from the same species abundance distribution for each treatment. Observed  $R$  values falling outside the expected range appear in boldface.

examples of neutral changes in species composition. Neutrality was not, however, confined to tied treatments, indicating that it may have a role in natural communities attached to maerl.

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

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

#### ACKNOWLEDGMENTS

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

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#### APPENDIX A

Location of field sites in Strangford Lough, Northern Ireland (*Ecological Archives* E090-036-A1).

#### APPENDIX B

Artificial stabilization treatments showing maerl tied to plastic mesh (*Ecological Archives* E090-036-A2).