Environment, not characteristics of individual algal rafts, affects composition of rafting invertebrate assemblages in Irish coastal waters

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ABSTRACT: The assemblage of marine invertebrates associated with floating macroalgal rafts may potentially be structured by ecological interactions and the characteristics of the rafts themselves. Alternatively, the assemblages might reflect a random process of colonization and loss from fragments, such that there is no systematic variation in assemblage structure with raft type. Analyses of 51 rafts collected from Irish coastal waters found no evidence for consistent patterns in the occurrence of species with raft size or algal composition. The observed patterns could not be distinguished from the predictions of a model with random allocation of individuals to rafts. Invertebrate species richness increased with raft size, but a multivariate test showed that this pattern was not associated with consistent changes in the identities of species found. Macroinvertebrate species assemblages were not significantly structured by the different species of algae in the raft. In contrast, the environmental variables at the point of raft collection, along with location data, were associated with variation in the species composition of rafts. The absence of any systematic structure related to raft size or composition in the sampled rafts suggests that, for the region studied, processes of raft break-up and coalescence obscure any potential effects of ecological interactions on individual rafts. The location-related variation in rafting invertebrate populations may reflect spatial variation in source populations or environmental factors that alter species compositions independently of raft type.

KEY WORDS: Metapopulation · Fragments · Coalescence · Dissimilarity · Null model · Passive sampling

INTRODUCTION

Naturally occurring and artificial floating rafts represent an important marine resource, potentially providing food, shelter, and opportunities for dispersal at the sea surface (Thiel & Gutow 2005a, Vandendriessche et al. 2006a). Rafting on floating material could potentially transport marine species beyond their existing biogeographical range (Barnes & Milner 2005). The movement of rafts plays roles in the transport of biomass and population connectivity at a range of scales (Helmuth et al. 1994, Wernberg et al. 2006, Fraser et al. 2011). The biota of rafts is shaped by processes of recruitment and population demography on floating material (Thiel & Gutow 2005a, Gutow et al. 2009). Some rafting species may have preferences for different types of algae in the raft (Vandendriessche et al. 2006b). Furthermore, there may be ecological interactions among rafting species that shape the composition of the rafting assemblage (Thiel & Gutow 2005a). The strength and types of ecological interactions on rafts are important as these can potentially alter the rafting assemblages and, therefore, affect the species that

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benefit the most from this habitat and from raft-assisted dispersal.

A conceptual model for the successional change in species composition on floating rafts was described by Thiel (2003). This model consisted of a subdivision of algal raft assemblages into 3 temporal phases: an initial phase where organisms associated with the algae before detachment are lost; a colonization phase where larvae or adults of new species arrive on the raft; and a local recruitment phase if organisms have been associated with the raft long enough to reproduce (species with direct development or asexual reproduction should be favoured during this stage). This model is explicit in describing how the outcomes of biotic interactions like competition and predation 'will determine which organisms persist on floating substrata' (Thiel 2003, p. 55). Vandendriessche et al. (2006b) concluded that the raft composition (*Sargassum muticum* dominance compared to *Fucus vesiculosus/Ascophyllum nodosum*) could also affect the densities and richness of associated macrofauna.

To evaluate the potential role of ecological processes on rafts, a relevant null model needs to be articulated. A null model deliberately excludes the processes of interest (in this case habitat preferences and ecological interactions) to determine the probability of the observed patterns occurring in the absence of the excluded processes (Gotelli 2001). In the absence of habitat preference and ecological interactions, the null expectation is that individuals, regardless of species identity, are randomly allocated to rafts, only restricted by the number of individuals on each raft. Assuming a large raft supports more individuals and individuals are allocated to rafts randomly, then a higher species richness is expected on large rafts. Under a null or random sampling expectation, however, a larger raft would have more species than a small raft but would not host species found exclusively on larger rafts. Association of a species with a particular raft type is evidence for some sort of ecological structuring through habitat preference or ecological interaction. Similarly, the simplest model for the abundance of a species is that there is an average density per unit mass of algae. Hence a large raft will hold more individuals of a species, but the abundance per unit mass will be constant across rafts. Again, habitat preferences, raft-size specific demography or ecological interactions may cause deviations from a simple abundance per unit mass relationship.

We examined the structure of macroalgal rafts and their associated fauna using samples collected from a cruise around the coast of Ireland, from Galway on

the west coast to the Celtic Sea front (between Ireland and Wales). This permitted sampling of rafts separated by as much as 579 km of coastal water. Rafts were sampled near the shore (400 m) and at distances exceeding 30 km from the shore in frontal waters. The null model, that raft assemblages are drawn from the same pool of species was tested using multivariate tests, with the alternative hypotheses being that raft assemblages are differentiated by environmental conditions and/or the raft size and composition. Species abundances (no. of ind. 100 g^{-1} raft) were also tested for evidence that population densities vary between rafts of different sizes.

MATERIALS AND METHODS

Collection and treatment of rafts

Rafts were collected from the RV 'Celtic Voyager' during a cruise from 13 to 22 June 2009. The cruise started in Galway before moving south along the coast and towards the Irish Sea (Fig. 1). A total of 51 rafts were collected, made up of 20 identified algal taxa (Table 1). As more than 1 raft may have been picked up when the ship stopped, there were 20 different sample locations. The 2 easternmost rafts were collected north of the Celtic Sea front in water with a temperature of 12°C, cooler than all other samples

Table 1. Macrophyte species identified from rafts

| Macrophyte species	Frequency in rafts (%)	Wet weight of species (g, n = 51) Mean	SE
Ulva spp.	98	138.768	42.127
Chorda filum	80	15.947	5.685
Ascophyllum nodosum	76	195.165	48.510
Fucus vesiculosus	76	126.184	34.194
Sargassum muticum	67	10.202	3.577
Fucus spiralis	57	2.231	1.368
Cystoseira spp.	57	64.351	22.591
Polysiphonia lanosa	53	3.147	0.981
Halidrys siliquosa	43	0.810	0.415
Himanthalia elongata	41	67.650	19.749
Asperococcus spp.	37	1.744	0.846
Zostera marina	33	0.338	0.148
Pelvetia caniculata	25	3.395	1.630
Leathesia difformis	22	0.162	0.070
Osmundea pinnatifida	8	0.491	0.444
Laminaria spp.	6	0.761	0.623
Scytosiphon lomentaria	6	0.043	0.025
Fucus serratus	4	0.537	0.524
Fucus ceranoides	4	2.876	2.045
Mastocarpus stellatus	2	0.003	0.003
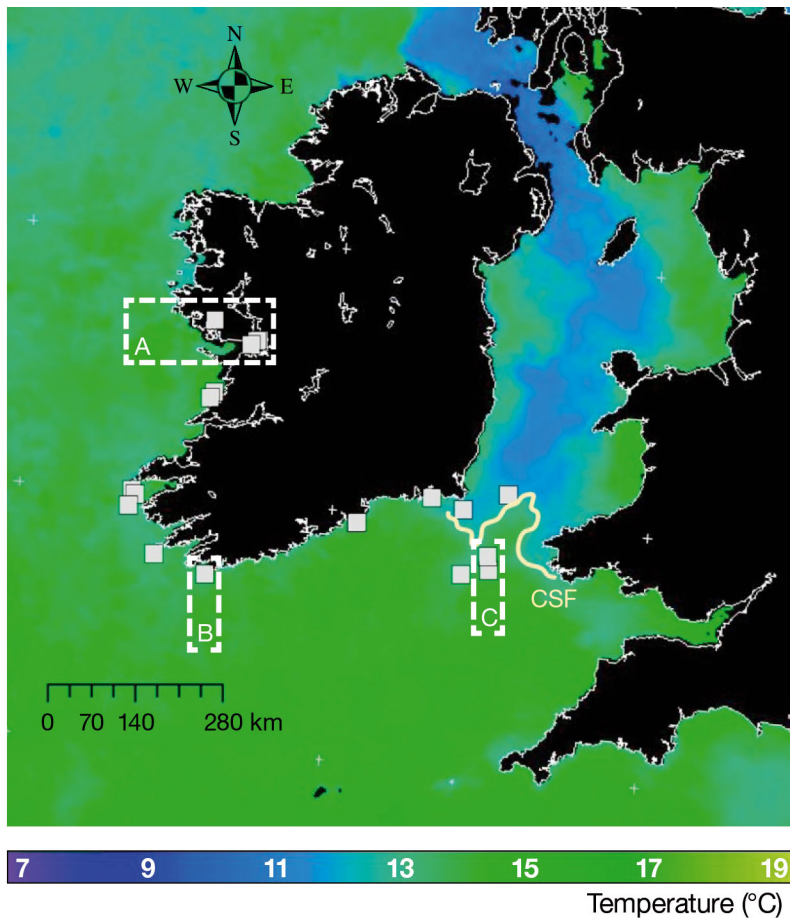
Fig. 1. Sampling locations (▪) for rafts around the coast of Ireland. Temperature shown is the 'level 3' weekly composite of AVHRR satellite-sensed sea surface temperature for June 14–June 20, 2009. The position of the Celtic Sea Front (CSF) is indicated, approximately separating cool Irish Sea waters (≤12°C) from the warmer Celtic Sea (> 12°C). Regions referred to in the text are indicated as (A) Galway Bay, (B) off Clear Island and (C) Celtic Sea warm water

a large fume hood. The 4% formaldehyde-seawater was drained over a 500 µm sieve, and all animals picked from the algae were placed in a sorting tray filled with seawater. As the focus of the study was on a null model involving random allocation of individuals to rafts, colonial species (where it is difficult to assign individuals) were not recorded. Organisms were sorted into major groupings and preserved in 74% industrial methylated spirits and seawater for further identification. Algal species forming each raft were surface-dried with absorbent paper towels for wet weight measurement, and their condition was noted. All animal species were sorted and identified to species level where possible following Hayward & Ryland (1995), Tebble (1966) and Graham (1971).

Test of asscociations between rafts and species

A multivariate approach was used to describe the variation among raft macroalgae and among raft-associated assemblages. Compositional differences (flora and fauna) between pairs of rafts were summarised using Simpson's dissimilarity coefficients (Koleff et al. 2003). This coefficient is 0 when assemblages on separate rafts are identical and scaled to 100 when there are no species in common between separate rafts. An important feature of Simpson's dissimilarity is that it measures compositional turnover, but is not affected by differences in species richness. Hence, 2 rafts with, for example, 10 species on one raft and 20 on the other can have a dissimilarity of 0 if the 10 species on one raft are all found on the other raft. In other words, if the less species-rich raft is effectively a subsample of the richer raft, the dissimilarity is 0. With other coefficients, including the commonly used Sørensen coefficient, the dissimilarity in rafts in the hypothetical example will not be 0, potentially leading to the artificial inference that the smaller raft has a fundamentally different assemblage composition when compared to the larger raft. The PRIMER software used for multivariate analysis

(mean temperature: 13.8°C). Rafts were collected between 0.4 and 61.4 km from land.

Rafts were collected using observers on the bridge of the ship to identify floating seaweed patches ahead of the vessel track. When rafts were spotted the ship was manoeuvred gently towards the clumps. Rafts were carefully collected in a large aperture dip net (80 × 80 cm, mesh size 0.25 cm). Sampled rafts were preserved in sealed buckets with 4% formaldehyde in seawater; seawater rather than freshwater was used to minimize osmotic damage to fixed material. Sea surface temperature, salinity and fluorescence were measured adjacent to sampling locations with a Seabird 911plus CTD array lowered from the ship. All preserved material was taken onshore for processing in the laboratory. Each sample was processed within

does not calculate Simpson's dissimilarities, so these were calculated from species presence-absence data in EXCEL using the PopTools add-in (Hood 2010) and dissimilarity matrices were subsequently imported into PRIMER for statistical tests.

Environmental variation among the locations where rafts were collected was summarized using principal components (PCAs). To add to the variables measured by the CTD array—sea temperature (°C), salinity, chlorophyll fluorescence (mV) and dissolved oxygen concentration (ml per cubic decimeter, dm^{-3}) —the following location variables were also measured: linear distance from shore (km), Irish Grid Easting (m) and Irish Grid Northing (m). Ranges for the CTD-measured variables were temperature 12 to 15.4°C, salinity 33.8 to 35, chlorophyll fluorescence 0.1 to 0.2 mv and dissolved oxygen concentration 3.8 to 6.3 ml dm^{-3}. Linear distance from the shore was included as a possible measure of time at sea, and hence a potential predictor variable of species turnover according to Thiel's (2003) model. A further potential influence on raft assemblages is the fraction of buoyant algal species in rafts. If floating species are more likely to sustain rafts at sea, then a higher fraction of floating algal species may lead to greater species densities or diversities, or may be associated with other successional changes. The division into floating or non-floating algal species was made on the basis of the presence of air bladders.

Tests of the associations between raft macroalgal composition, raft faunal assemblage composition and raft size were made using the RELATE procedure in PRIMER. The RELATE test is a non-parametric Mantel test that evaluates the association between different dissimilarity matrices. The algorithm randomly permutes dissimilarity values so that the observed rank correlation between matrices can be compared to the values expected under a null hypothesis of no underlying association. RELATE tests were carried out between dissimilarity matrices. To make comparisons with variables summarised by principal component analysis (PCA), the RELATE tests used dissimilarities based on the Euclidian distance between points along each PC axis.

Univariate correlations were used to compare among species richness with raft characteristics. Spearman's rank correlations were used to avoid ambiguity in deciding which transformation was appropriate for nonlinear relationships.

The hypothesis that the density of each species can be summarised using a constant abundance per unit raft mass was tested using the abundance count for each species divided by the total wet weight of the algae in the raft. These values were multiplied by 100 to give 51 values for the number of individuals of a species per 100 g of raft. If a species is relatively more abundant at particular sizes of raft, then a correlation is predicted between density of individuals and raft size. Correlations for this test were parametric (Pearson's r) as the hypothesis concerns variation about the mean. Plots were examined for nonlinearity by testing the significance of polynomial regressions.

RESULTS

Rafts varied in size from 12 to 4688 g wet weight (mean: 639, SE: 128.0). The green algal group identified as *Ulva* spp. was the most frequently encountered taxon, but brown algae dominated in biomass terms. Five taxa accounted for 93% of the biomass collected: *Ascophyllum nodosum*, *Ulva* spp., *Fucus vesiculosus*, *F. spiralis* and *Himanthalia elongata*. Crustacea made up the majority of marine invertebrates associated with rafts (over 90% of invertebrates counted), with *Idotea baltica* found on almost all rafts (Table 2).

Large rafts tended to have more species (Fig. 2). Both algal species richness (Spearman's r = 0.516) and associated marine invertebrate richness (Spearman's r = 0.507) were significantly correlated with the wet weight of rafts (p < 0.01 in both cases). Larger

Table 2. Marine invertebrate taxa found on >10% of rafts sampled

Invertebrate taxon	Frequency on rafts (%)	Density (no. of ind. 100 g^{-1} raft, n = 51) Mean	SE
Idotea balthica	96	3.7	0.52
Gammarus locusta	88	24.5	6.85
Idotea spp.	86	9.6	2.74
Brachyura spp. megalopae	67	10.5	5.72
Idotea neglecta	59	1.7	0.51
Idotea granulosa	45	0.4	0.11
Idotea emarginata	45	0.4	0.10
Liocarcinus holsatus	39	1.1	0.43
Mytilus edulis	29	0.4	0.16
Jassa falcata	27	0.3	0.20
Jaera sp.	25	0.3	0.09
Spirorbis spp.	22	3.5	1.96
Platynereis dumerilii	22	0.3	0.11
Liocarcinus spp.	18	0.1	0.05
Idotea pelagica	18	0.1	0.09
Polychaete larvae	16	0.2	0.11
Littorina obtusata/fabalis	16	0.1	0.07
Anomura spp. megalopae	12	5.7	3.27

rafts tended to carry a greater number of individual animals, regardless of species (Fig. 2c; Spearman's r = 0.378, p < 0.01). While large rafts tended to host larger populations of invertebrates, the densities of individual species did not vary as a function of raft size: all correlations between the abundance of a species (listed in Table 2) per 100 g of raft and raft weight (i.e. size) were not significant. Examination of the plots did not suggest that significant nonlinear relationships existed.

The locations and conditions of where rafts were sampled are summarised using a PCA in Fig. 3. The regions highlighted in Fig. 1 are evident in the plot

using all the data (Fig. 3a). The PCA loading plot emphasizes that rafts from Galway Bay cluster as the most northerly samples, but also are of relatively low salinity and contain a slightly higher fraction of positively buoyant algal species (i.e. they contained air bladders). Aside from the group of coastal samples with no clear geographic structure, those in the vicinity of Clear Island and from the Celtic Sea stand out. The Celtic Sea rafts were sampled in warmer water with relatively low chlorophyll fluorescence and dissolved oxygen. These tended to be slightly larger rafts. In the vicinity of the front, relatively small geographic separations could make quite a difference to the environmental variables. For example, the sample location closest to, but not in, region C (Celtic Sea Warm water) appears to reflect an intrusion of cooler Irish Sea water, with a temperature of 14.1°C compared to a temperature of 15.4°C at the adjacent locations. Rafts from near Clear Island appeared associated with waters of higher salinities and phytoplankton concentrations than other areas. Dissimilarities among rafts on the PC axes were associated with variation among invertebrate assemblages. The association between position on the second PC axis and invertebrate dissimilarity was significant (RELATE test, Spearman's r = 0.25, p < 0.05).

The first panel in Fig. 3 contains both location-specific details and information specific to each raft. These variables were analysed separately. Not surprisingly, a PCA based on location-specific information continued to emphasise the regional distinctiveness of Galway Bay, Clear Island and warm Celtic Sea samples (Fig. 3b). Again, differences among raft scores along PC axis 2 were related to dissimilarities in the invertebrate assemblage (RELATE test, Spearman's r = 0.20, p < 0.05). Unsurprisingly, there was less geographic structure found to be based on the 3 variables of raft size, the fraction of floating algal species and the distance from land (Fig. 3c). The Galway Bay, Clear Island and Celtic Sea sample groups were closer in the PCA, with some overlaps (Fig. 3c). The association with invertebrate dissimilarity in rafts was not maintained in the PCA based on the 3 variables. Variation in raft size, the fraction of floating algal species and the distance from land was not related to the Simpson's dissimilarities in invertebrate assemblages (RELATE test, best Spearman's r with any PCA axis = 0.05, p > 0.05). The relationship between the algal composition of a raft (Simpson's dissimilarities) and the structure of the associated invertebrate assemblage was also not significant when tested using a RELATE test (Spearman's r = 0.07, p > 0.05).
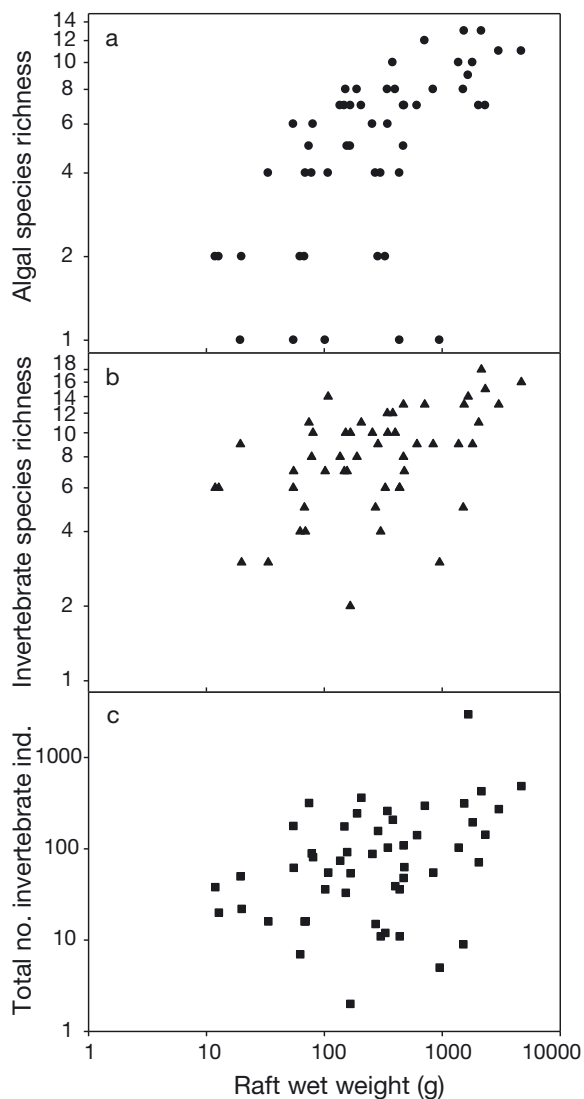

Fig. 2. Relationships between (a,b) species richness or (c) total invertebrate abundance and total raft wet weight. (a) Macrophytes, (b) marine invertebrates. All 3 relationships were significant (Spearman's correlations p < 0.01)
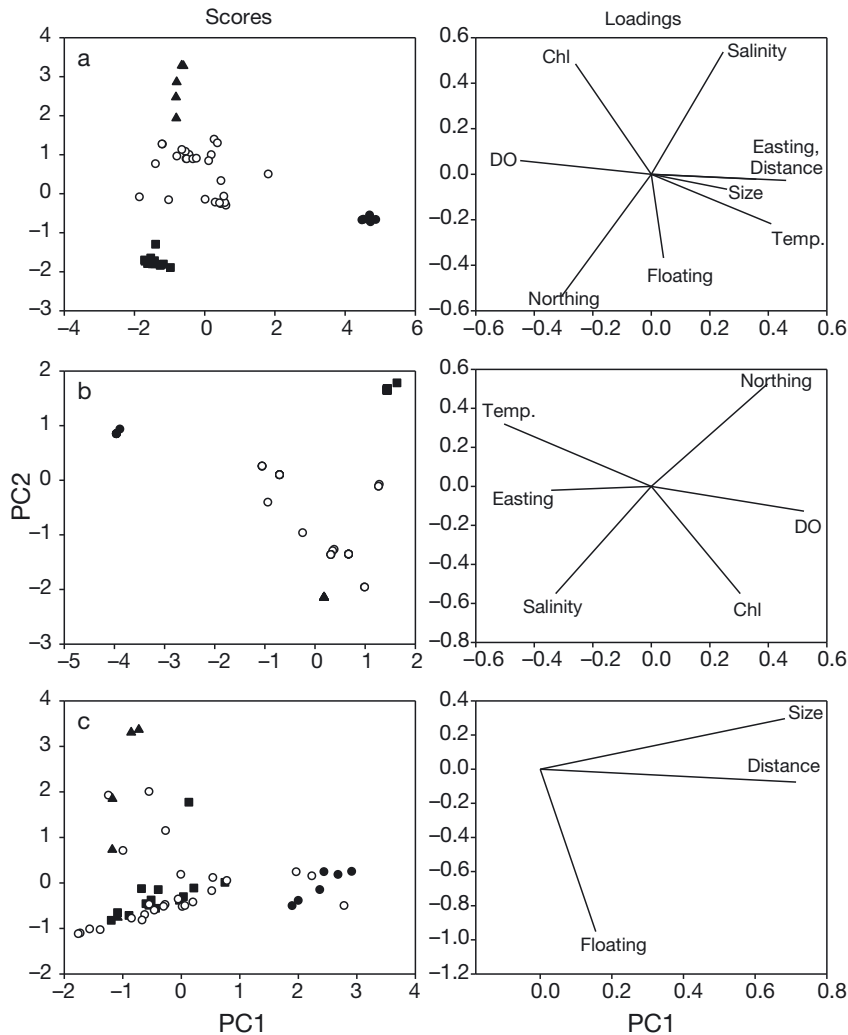
Fig. 3. Principal component (PC) analysis ordinations (scores, left-hand panels) of rafts with accompanying loading plots (right-hand panels) showing the orientation and magnitude of loading for different variables. (a) All variables (sea temperature, Temp.; salinity; chlorophyll fluorescence, Chl; dissolved oxygen concentration, DO; linear distance from shore, Distance; Irish Grid Easting, Easting; Irish Grid Northing, Northing; raft size, Size; and fraction of floating algal species of total in raft, Floating). (b) Variables related to sample location and associated environmental conditions and (c) variables reflecting raft features and a proxy for raft age (Distance). Percent of the multivariate variation explained by the first 2 components as follows: (a) 63%, (b) 78% and (c) 87%. Sample locations relative to the boxes in Fig. 1 are shown — ■: Galway Bay; ▲: off Clear Island; ●: Celtic Sea warm water. ○: all rafts falling outside the boxes in Fig. 1

DISCUSSION

The patterns of invertebrate assemblage structure were consistent with the predictions of a null model: the species found on rafts reflect random subsamples of the same pool, with no consistent ecological structuring. There was no evidence that species were more likely to occur on particular sizes or types of rafts. Furthermore, the population densities of differ-

ent species did not vary consistently with raft size.

Apparently unstructured raft assemblages contradict previous studies that have suggested a role for ecological processes such as habitat associations or competition and predation on rafts. Three possible, and non-exclusive, explanations for such a contradiction are that: (1) the analytical approach (using RELATE tests) was not powerful enough or lacked some appropriate predictor variables of raft composition; (2) previous studies did not test an appropriate null model or the evidence for ecological structuring of raft assemblages was weaker than concluded for some other reason; or (3) ecological structuring is variable in space and time with the rafts in the current study, reflecting a situation of weak or absent structuring.

Using the RELATE statistical approach, we were able to link spatial variation in rafts with compositional variation in the associated invertebrate assemblages, suggesting that the absence of a link to raft variables was not just due to a lack of statistical power. A number of alternative approaches were attempted to link the composition and abundance of algae in rafts to the associated fauna. Similar to the RELATE tests, these alternative approaches did not produce results indicating an ecological structuring of raft assemblages. These approaches included multivariate regression trees (De'ath 2002), which can identify any structure in the invertebrate assemblages associated with particular algal species. Models with the biomass of individual algal species entered as predictor variables had poor predictive power and did not describe variation in invertebrate assemblage composition (cross validation errors > 1, see Supplement at www.int-res.com/articles/suppl/m470p031_supp.pdf). Similar to the RELATE tests using PCA-derived variables, spatially-related information could be used in multivariate regression trees to model variation in raft invertebrate assemblages.

A number of studies that have found differences in raft-associated species with raft type may provide weaker evidence for ecological structuring due to oversights in analysis or interpretation. For example, although Stoner & Greening (1984) concluded that there were differences in the assemblages on *Sargassum* spp. rafts classified into different age classes, they did not formally test this interpretation. The data in Tables 7 & 8 of Stoner & Greening (1984) can be tested by randomly reallocating individuals to raft classes. The data from their Table 7 (Gulf Stream rafts) do not have a pattern that differs significantly from a random allocation of individuals to rafts (Table 3 of the present study). Similarly, there is no formal test of the differences in expected species number between rafts dominated by *Sargassum muticum* or *Fucus vesiculosus/Ascophyllum nodosum* in Vandendriessche et al. (2006b). The multivariate tests of Vandendriessche et al. (2006b) used the Bray-Curtis similarity measure. Unfortunately, this measure does not unambiguously resolve differences in abundance from differences in composition (although note that the original application used standardization of counts to percentages, which partially avoids this issue; Bray & Curtis 1957, Yoshioka 2008). Without standardization, the Bray-Curtis dissimilarity between 2 samples with identical relative distributions of species, but where the samples differ in absolute number of individuals, is not 0. Therefore, 2 rafts of different sizes and different numbers of associated individuals will never have a dissimilarity of zero even where the relative abundances of species are identical across rafts. The use of the Bray-Curtis measure means that the multivariate results of Ólafsson et al. (2001) and Vandendriessche et al. (2006b) cannot be used to unambiguously test whether a model of random allocation of individuals could have caused the observed patterns. Other support for distinct associations with raft characteristics is weak. Hobday (2000) tested 19 species occurrence patterns on a case-by-case basis and found only one reflected changes in raft age.

In the current study, the assemblages were tested against raft size rather than age. It may be that age, in many circumstances, is a more appropriate structuring variable. For the coastal rafts sampled around Ireland, however, it was not possible to estimate raft age. The rafts were made up of an average of 8 algal species (SE: 0.53) and it was not possible to age them based on general condition of the material. The majority of species in rafts had air bladders (mean: 5.9 species with air bladders in each raft). The mixed raft composition is likely to have reflected the turn-

Table 3. Distribution of individuals by species in *Sargassum* rafts of different age classes sampled by Stoner & Greening (1984; see there for species references). Expected values were generated by randomly assigning observed individuals to a raft category 1000 times. (a) Data for Gulf Stream rafts, 900 ind., $\chi^2 = 20.81$, χ^2 critical ($\alpha = 0.05$) = 68.34, non-significant. (b) Data for Sargasso Sea rafts, 888 ind. $\chi^2 = 103.56$, χ^2 critical ($\alpha = 0.05$) = 59.13: p < 0.05. Critical values of χ^2 were generated by randomising the location of individuals 999 times using PopTools

Species reference	Rafts observed			Rafts expected		
	Young	Mid	Old	Young	Mid	Old
(a) Gulf Stream rafts						
S1	19	571	20	23.6	568.0	18.3
S2	6	83	1	3.6	83.8	2.7
S3	2	49	1	2.0	48.5	1.5
S4	1	39	1	1.7	38.2	1.3
S5	4	26	3	1.2	30.7	1.0
S6	2	18	0	0.8	18.6	0.6
S7	1	18	1	0.8	18.6	0.6
S8	0	12	0	0.5	11.2	0.4
S9	0	8	0	0.3	7.5	0.3
S10	0	5	0	0.2	4.6	0.1
S11	0	3	0	0.1	2.8	0.1
S12	0	2	0	0.1	1.9	0.1
S13	0	2	0	0.1	1.9	0.1
S14	0	1	0	0.0	0.9	0.0
S15	0	1	0	0.0	0.9	0.0
(b) Sargasso Sea rafts						
S1	10	130	83	25.6	136.8	60.7
S2	42	115	43	22.8	122.7	54.1
S3	10	67	28	12.1	64.4	28.5
S4	15	52	27	10.7	57.7	25.5
S5	5	59	13	8.8	47.3	20.8
S6	7	53	5	7.6	39.9	17.6
S7	4	16	13	3.8	20.4	9.1
S8	2	9	12	2.7	14.0	6.2
S9	4	7	3	1.6	8.5	3.8
S10	1	11	1	1.5	8.0	3.6
S11	0	3	6	1.1	5.5	2.4
S12	2	5	1	0.9	4.9	2.2
S13	0	5	0	0.6	3.2	1.3
S14	0	4	0	0.5	2.5	1.1
S15	0	2	1	0.4	1.9	0.8
S16	0	2	1	0.4	1.8	0.8
S17	0	2	1	0.4	1.9	0.8
S18	0	0	2	0.2	1.2	0.6
S19	0	2	0	0.2	1.2	0.5
S20	0	0	1	0.1	0.6	0.3
S21	0	1	0	0.1	0.6	0.3

over of material joining and leaving clumps, making it difficult to assign a specific age to each raft. As in other studies (e.g. Tsikhon-Lukanina et al. 2001), the presence of particular species may indicate the age of fragments. For example, the pelagic barnacles *Dosima fascicularis* and *Lepas anatifera* reflect material that has been at sea long enough for recruitment of these species to occur. However, these species

were only found on 2 rafts in the current study and the invertebrate assemblages on these 2 rafts were not distinct from other samples (ANOSIM test in PRIMER, not significant).

An alternative line of evidence for evaluating any changes in raft assemblage with size or age of raft is to examine patterns in density (individuals per unit mass or volume). There were no relationships between density and raft size for any species on Irish coastal rafts. Other authors have, however, reported significant relationships in other regions: Hobday (2000) found 9 significant density–age relationships out of 74 tests; Ingólfsson (1995) identified 23 significant rank correlations between density and raft size in approximately 110 species–region combinations, and Vandendriessche et al. (2006b) report around a third of taxa with a significant correlation between density and raft volume. Despite some potential issues with multiple hypothesis testing, the association of species' densities with raft characteristics, these previous studies suggest that some structuring is possible.

The third possibility to consider is that the strength of ecological structuring varies in space and time and that the rafts sampled in Irish coastal waters reflect a situation where habitat preferences and ecological interactions are weak. There is certainly evidence from other studies that ecological structuring of raft associated assemblages can vary in strength. For example, while Stoner & Greening (1984) report some data (their Table 7) that was consistent with a random allocation of individuals to rafts, further data in their study (see their Table 8, Sargasso Sea rafts) shows evidence for different assemblage composition in the different age classes of raft (see also Table 3 of the present study).

The evidence from Irish coastal rafts examined in the current study implies that there are no clear interactions that shape the raft assemblages. This situation may reflect the continual breakup and coalescence of macroalgal rafts and raft fragments as observed at similar distances from the shore by Ingólfsson (1998). Movement of algal fragments among rafts will disrupt ecological structuring processes. The rafts in the current study were all collected within 62 km of a coastline, and, thus, it may also be the case that the rafts have not had sufficient time for ecological interactions to shape the composition of the associated assemblage. The rafts sampled might still receive frequent immigrants from recently detached coastal rafts. Only rafts at larger distances from the coast, might experience successional changes, e.g. due to loss of coastal species (see Ingólfsson 1995, Gutow et al. 2009) or due

to greater opportunities for colonization by pelagic species (e.g. lepadid barnacles; Macaya et al. 2005).

If the patterns observed on Irish coastal rafts represent turnover and exchange of materials among rafts such that potential ecological structuring processes are weakened, then rafts less subject to breakup and coalescence may be expected to provide better evidence for processes like competition and habitat preference. For example, artificial floating materials seem less likely to coalesce, with individual floating items less likely to break-up and with longer periods at sea than algal fragments. This can lead to differences in the assemblages on different floating materials dependent on the likelihood of positional changes (Bravo et al. 2011). Tsikhon-Lukanina et al. (2001) showed changes in assemblages between rafts of different age classes (on the basis of *Lepas* sp. size categories). Macrophyte rafts made up 15% of those studied, but it was not reported whether the assemblage structuring was stronger or weaker on algal rafts in comparison to those of wood or plastic (Tsikhon-Lukanina et al. 2001). Even when only considering macroalgal rafts, there are likely to be spatial variations in rafting processes and timescales, which will cause variation in the strength of ecological structuring between studies.

Spatial variation in raft assemblages is not explicitly predicted by the succession model, which is more concerned with the turnover of species as a raft ages (Thiel 2003). The exception to this would be where the spatial variation also reflects raft age. This seems to be unlikely in the current study and perhaps the most likely covariate with raft age (distance from shore) was not related to variation in raft assemblage structure. The spatial variation in raft assemblages may, however, reflect variation in the nearby source populations. Alternatively, variables like temperature may affect the persistence of particular species, leading to spatial differences among rafts, but independently of the composition or size of individual rafts. For some variables, like chlorophyll fluorescence, the link to the persistence of different species is difficult to make. However, as there are correlations among the different environmental and spatial variables, it is difficult to estimate what may be the key drivers of any spatial variability in species composition.

The patterns found in the present study of Irish coastal rafts imply that the characteristics of individual rafts may not be the key drivers for the ecology of the system. The individual rafts in this case do not have a clear identity for prolonged periods of time as they are constantly losing and gaining material. A

view of rafts as transient entities, frequently coalescing and fragmenting, implies that larger scale processes that affect the interaction rates among rafts will assume a greater importance. As has already been suggested for *Sargassum* spp. (Stoner & Greening 1984), processes such as the formation of windrows or other areas of aggregation will affect the transfer of individuals across rafting materials. The rafting community may therefore be partially structured by the frequency and extent of zones of aggregation at the ocean surface. Furthermore the total amount of material at sea may affect the persistence of associated species by metapopulation-like processes. The raft system is not a classical metapopulation (Levins 1969) as rafts are not fixed patches of habitat. However, at any one point in time, each raft can be occupied (or not) by a species and processes of extinction and colonization can occur. This suggests that metapopulation predictions are valid, including that a threshold number of rafts exists below which long term species persistence is not possible in the system (Hanski et al. 1996). If the total amount of rafting material is more important than the characteristics of individual rafts, then the neuston net approach of Davenport & Rees (1993) may be a more appropriate method to study raft system dynamics at larger scales. A prediction of the threshold habitat concept would be that large scale gradients in raft biomass (a peak at mid-latitudes, Thiel & Gutow 2005b) will be reflected in gradients of richness in the associated fauna, with some species characteristically becoming absent in areas of low raft density.

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