East-west spatial groupings in intertidal communities, environmental drivers and key species

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The rocky intertidal communities of Ireland contain a mix of cold- and warm-adapted species, however the spatial distribution of these communities has not been investigated in a systematic way. Based on a benthic community dataset collected in 2003 at 63 sites, several statistical analyses were combined with the aims of (i) detecting groups of similar communities and their spatial arrangement, (ii) relating these groups to environmental factors and (iii) identifying the species that drive the different community groups. Sørensen's index suggested two marine community groups, one of the east and south-east (termed 'east') and the other in the west, south-west and north (termed 'west'). A second partition based on combined wave exposure and sea surface chlorophyll comprised four groups, as did a further partition based on combined sea surface and air temperatures. The spatial arrangement of wave height plus chlorophyll conditions agreed reasonably well with the binary marine community partition, but the temperature partition did not. The 'east' community appeared to be associated with low wave height and chlorophyll conditions. The species that were most influential to the 'east' community were Balanus crenatus, Austrominius modestus and Fucus vesiculosus. The 'west' sites were associated with high wave height/low chlorophyll (with some variation in this due to local shelter) and the species Paracentrotus lividus, Chthamalus stellatus, Alaria esculenta and Himanthalia elongata. A longitudinal pattern rather than one associated with latitude was evident in this marine community and local drivers rather than temperature clines appeared most important for the dominant community patterns.

Keywords: Rocky shore community, similarity index, cluster analysis, wave exposure, chlorophyll a, climate change, algae, macroinvertebrates

Submitted 13 May 2016; accepted 13 September 2016; first published online 25 October 2016

INTRODUCTION

Environmental conditions in intertidal habitats vary sharply, but predictably, to give rise to strong marine community patterns (Ballantine, 1961). The interplay of predictable tides and associated abiotic pressures, along with biological structuring mechanisms, i.e. grazing, competition, predation and recruitment (Connell, 1985; Gaines et al., 1985; Power et al., 1999), gives rise to an intertidal zonation of macroinvertebrates and algae. This has been suggested to be universally apparent (Stephenson & Stephenson, 1949; Lewis, 1964) or, at least, consistent at regional scales (Ingólfsson, 2005). Because of these strong environmental and community gradients, exceptional accessibility, and intensively studied ecology, intertidal habitats are an established sentinel system for monitoring

climate change in the marine realm (Barry et al., 1995; Helmuth et al., 2002; Hawkins et al., 2008; Pitt et al., 2010).

The impetus to investigate the impacts of global warming has led to more detailed understanding of thermal tolerance and its biochemical basis in individuals, or more generally, in ectotherms (Pörtner, 2001, 2010; Deutsch et al., 2015). But how the integrated effect of metabolic and biochemical responses to temperature variability is ultimately reflected in each species' distribution and abundance at broad spatial scales, is difficult to disentangle (Lewis, 1996). Conspicuous and easily identified rocky intertidal 'indicator' species are good candidates to track change, although complex interactions can also be expected to frustrate this process (Lewis, 1996). For example, focusing on particular indicator species may be confounded by their interaction with other community members who themselves are subject to unrelated effects, e.g. species which may be fluctuating in abundance due to harvesting, or human interference. Furthermore, at the scale above 'indicator' species, the question arises whether there are entire communities which can be linked to abiotic variables (e.g. Valdivia et al., 2015), say at the

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scale of a national coastline? If so, might it be possible to identify these communities for future monitoring?

Recent research acknowledges that global warming is only one of several man-made impacts on coastal systems, which are subjected to so-called 'multiple stressors' (Firth & Williams, 2009). An example of this would be the fact that many macroalgal species are commercially harvested for hydrocolloid production, human consumption or biofuels, although the latter are still at the development stage (Werner & Kraan, 2004; Bruton *et al.*, 2009; Singh *et al.*, 2011). Since algal biomass extraction in Europe is almost completely from wild algal stocks rather than cultivated stocks (Bruton *et al.*, 2009), this presents a threat to coastal communities. Macroalgae abundance, particularly *Laminaria hyperborea*, has been linked to the abundance of numerous subtidal species (Andrews, 1945; Moore, 1971, 1973), so much so, that the abundance of this algal species is a key predictor of community diversity (Burrows, 2012). Strong community effects have also been associated with *Ascophyllum nodosum* removal (Jenkins *et al.*, 2004). Other harvesting pressures in this habitat include fisheries for periwinkles *Littorina littorea* (Cummins *et al.*, 2002), urchins *Paracentrotus lividus* and *Mytilis* spp. (Fahy *et al.*, 2008). Understanding broadscale patterns in the occurrence of such species, along with their related communities, will aid mapping, management and protection of these important natural resources.

Directional change in the environmental conditions that influence intertidal habitats is expected to lead to biogeographic range shifts of species (Hiscock *et al.*, 2004; Power *et al.*, 2011), particularly in Britain and Ireland, where the North Atlantic Current allows southern (warm-adapted) species to coexist with boreal (cold-adapted) forms (Forbes, 1858). Simkanin *et al.* (2005) selected 53 rocky intertidal species which were classified as either 'northern' or 'southern' in biogeographic affinity; in addition, 'broadly distributed' species or those which provided 'contextual' information, e.g. keystone grazers such as *Patella* spp. (Hawkins, 1981; Firth & Crowe, 2008). Harvested species were also included, such as the algae *L. hyperborea* and *A. nodosum*, as well as shellfish such as *L. littorea* and *P. lividus*. After these species were surveyed at 63 Irish rocky shores in 1958 and again in 2003, a significant change in abundances of 12 out of 27 species was reported (Simkanin *et al.*, 2005). While this illustrated the dynamics of individual intertidal populations very well, the direction of change did not provide a clear link to global warming over the 45-year timeframe (Poloczanska *et al.*, 2013). An alternative question which may be asked of such a dataset is: what is the effect of environmental forcing on community patterns (as opposed to individual indicator species)? Understanding whether distinct communities occur and, if so, whether their spatial arrangement is linked to environmental variables, could be regarded as a useful step in understanding broadscale changes, such as those brought about due to climate.

The dataset from Simkanin *et al.* (2005) is also used in the present investigation; this time with the objective of examining spatial patterns in communities along the Irish coast. The first hypothesis which is tested is that there is no spatial pattern of distinct communities found on sectors of coast. The methods used to test this involve a computation of similarity matrices and a subsequent hierarchical agglomerative clustering of sites based on the complete linkage algorithm. Given that the assemblage sampled is a mixture of warm- and cold-adapted species, a second hypothesis tested is that there is no association between intertidal communities and trends in coastal temperatures. This is examined by clustering temperature signatures at all sites to examine whether the resulting partitions overlap with marine community trends. Besides temperature (Hiscock *et al.*, 2004), additional environmental factors which have been shown to play important roles in rocky intertidal community structure are also included in the present analysis, i.e. wave exposure (Rattray *et al.*, 2015) and eutrophication (Grall & Chauvaud, 2002). The final aim is to understand which species might be involved in any distinct spatial community groupings.

As well as providing a first look at the spatial arrangement of Irish intertidal communities, the knowledge obtained by our study could present advantages in the choice of future conservation and monitoring arrangements for the impacts of global warming. It could also help monitor activities such as coastal harvesting, which can have direct or indirect effects on many intertidal species.

MATERIALS AND METHODS

Datasets

Ireland's coastal habitats vary from sheltered rocky beaches to imposing wave-exposed cliffs along a coastline that is ~7524 km long and which is composed of rocky shores over 40% of that extent (Neilson & Costello, 1999). The present analysis is based on the raw dataset described in Simkanin *et al.* (2005) for a temporal analysis of change to the rocky intertidal community. This rocky shore community dataset comprises 63 sites all around Ireland (Table 1 and Figure 1), where 57 species were surveyed (Table 2). All fieldwork was carried out from March to November 2003 by the same two operators (i.e. no operator error across sites). Shores were sampled at low water during spring tides to allow for an adequate estimate of lower shore species. Community data were collected using an ordinal abundance scale, 'ACFOR', which included the following six categories: 'Abundant', 'Common', 'Frequent', 'Occasional', 'Rare' and 'not seen'. This scale was chosen to ensure that data would be comparable with the historical datasets of Southward & Crisp (1954) in Ireland and parallel studies in Britain (Crisp & Southward, 1958). Both operators spent an hour searching and recording abundances on each shore. Species were given an abundance score after 2 h of sampling effort and if a species was not found during that time it was recorded as not seen. The abundance of all species which were present was assessed in the 'zone of maximum abundance', according to pre-established sampling protocols of the MarClim project (Laffoley *et al.*, 2005). For the present analysis, the ordinal dataset was reduced to presence/absence only i.e. 'not seen' becomes 'absent' while all other categories become 'present'.

Four environmental parameters were examined at all 63 sites: sea surface temperature (SST), air temperature (AT), wave height (WH) and sea surface chlorophyll-a concentration (Chl-a). All environmental factors were standardized via z-scoring (subtraction of the arithmetic mean across sites and division by related empirical standard deviation) prior to statistical analysis, leaving one value per environmental factor and per site (see below).

Table 1. Field sites surveyed in 2003. Numbers correspond to Figure 1.

1. Culdaff, Dunmore Hd, Co. Donegal
2. Fanad Head, Co. Donegal
3. Bloody Foreland, N + S, Co. Donegal
4. Rinnalea Pt, Co. Donegal
5. Maghery-Termon, Co. Donegal
6. St. Johns Point, Co. Donegal
7. Easky, east of quay, Co. Sligo
8. Termoncarragh, Co. Mayo
9. Dooagh Achill Island, Co. Mayo
10. Cloghmore Achill Sound, Co. Mayo
11. Mannin Bay, Clifden, Co. Galway
12. Bunowen Point, Co. Galway
13. Black Head, Co. Clare
14. Cangregga, Co. Clare
15. Furreera, Co. Clare
16. Doonbeg, Co. Clare
17. Castle Point, Co. Clare
18. Moneen, Loop Head, Co. Clare
19. Kerry Head, Southside, Co. Kerry
20. Lough Kay, Doulus Bay, Co. Kerry
21. Portmagee Channel, Co. Kerry
22. Abbey Island, Derrynane, Co. Kerry
23. Daniels Island, Co. Kerry
24. Whiteball Head Bay, Co. Cork
25. Gyleen, Cork
26. Tranabo Pier, Cork
27. Toe Head, Cork
28. Toe Head Bay, Cork
29. Galley Head, Co. Cork
30. Ringalurisky Point, Cork
31. Old Head of Kinsale,Cork
32. Goleen, Co. Cork
33. Ballycotton, Cork
34. Knockadoon Head, Cork
35. Helvick Head, Cork
36. Bunmahon, Waterford
37. Brownstown Head, Waterford
38. Hook Head, Wexford
39. Baginbun Head, Wexford
40. Cullenstown Reef to W, Wexford
41. Forlorn Point/Crossfarnoge, Wexford
42. Carnsore Point, Wexford
43. Greenore Point, Wexford
44. Rosslare Harbour, Wexford
45. Cahore Point, Co. Wexford
46. Kilmichael Point, Co. Wexford
47. Ardmore Point, Co. Wicklow
48. Greystones, Co. Wicklow
49. Bray, Co. Wicklow
50. Skerries, Co. Dublin
51. Malahide Coast, Co. Dublin
52. Balbriggan, Co. Dublin
53. Port Oriel, Clougherhead, Co. Louth
54. Rosstrevor, Co. Down
55. Annalong, Co. Down
56. St. Johns Point, Co. Down
57. Kilclief, Co. Down
58. Kearney Pt, Co. Down
59. Townhead, Co. Down
60. Portmuck, Co. Antrim
61. Larne, Co. Antrim
62. Marconi's Cottage, Co. Antrim
63. Portrush, Co. Antrim

SST and AT data were obtained from the International Comprehensive Ocean-Atmosphere Data Set (ICOADs) provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, from their website at http://www.esrl.noaa.gov/psd/ (accessed 2.9.2015). These data are based on in-situ observations at a spatial resolution of $1°$ latitude $\times$ $1°$ longitude and averaged monthly temperature values (°C) from January 2000 to December 2003 inclusive, with coastal pixels being selected over the spatial extent $11-4°$ W and $51-56°$ N. The marine community will potentially be influenced by conditions during several years leading up to the period of field sampling in 2003, but many rocky intertidal species have life spans of between 3 and 25 years (Lewis, 1996); therefore four years of environmental data seemed a reasonable time-frame to choose in this context. To obtain a single value per site between 2000 and 2003, the SST or AT data were averaged for every site using the arithmetic mean before z-scoring.

Chl-a concentration (mg m^{-3}) data were obtained from Sea-viewing Wide Field-of-view Sensor (SeaWiFS). The data are a product generated by the NASA Ocean Biogeochemical Model (NOBM) based on data assimilation of remotely sensed Chl-a available on http://oceancolor.gsfc.nasa.gov/SeaWiFS (accessed 12.9.2015). As the monthly values were very patchy, the arithmetic mean values from 2000 to 2003 (inclusive) were also taken in this case, for every site.

Wave exposure was based on wave height as a proxy. Wave height (m) values spatially adjoin and assimilate the average observational data from satellite, ship and buoys and come from two different datasets: (i) Wave Energy Resource Atlas Ireland (2005) http://data.marine.ie/Dataset/Details/20929/ (accessed 18.11.2015) and (ii) Atlas of UK Marine Renewable Energy Resources (2008) http://www.renewables-atlas.info/ (accessed 18.11.2015).

Cluster analysis

Each cluster analysis built on pairwise distances between sites (organized in the form of a 63×63 symmetrical distance matrix). For the categorical ('absent', 'present') community data, we found the Sørensen(-Dice) similarity index SD most useful to compute a distance according to $\sqrt{1 - SD}$ (Borcard *et al.*, 2011). To check whether differences in species richness across sites could have influenced this analysis, corroboration was sought from an alternative distance metric, Raup–Crick dissimilarity, which was calculated according to the method of Chase *et al.* (2011) with 50,000 permutations (this metric is less sensitive than Sørensen's index to species richness).

For the environmental data metric we used the Euclidean distance. Before beginning the cluster routine, we performed correlations between all the environmental parameters using Spearman's rank correlation coefficient, to identify highly correlated factors, to simplify the clustering process. The result suggested clustering sites twice, separately with respect to pairs of environmental factors: (AT&SST) and (WH&Chl-a).

For the hierarchical agglomerative cluster algorithm, we chose the complete linkage method (Borcard *et al.*, 2011). Here the most distant pair of sites from two separate clusters is relevant for hierarchical agglomeration of these clusters. In comparison with alternative algorithms, e.g. single linkage clustering, (un)weighted average clustering, etc., this choice is most conservative. To find the optimal number of clusters we computed (i) the Mantel statistic and (ii) the silhouette
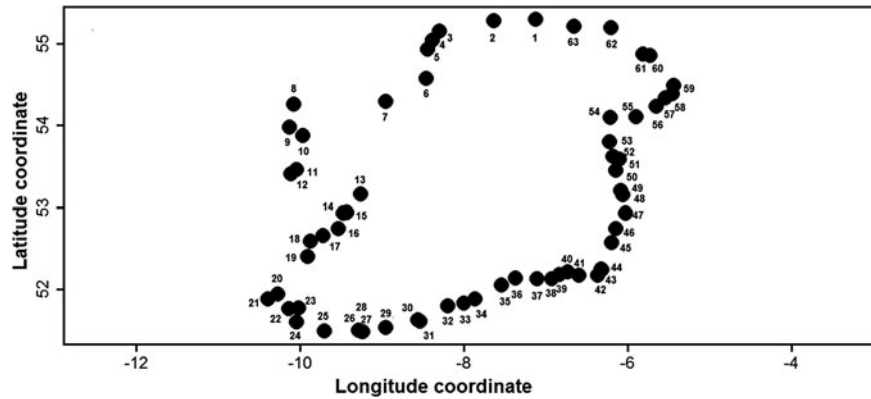
Fig. 1. Field sites around Ireland that were sampled in 2003 for 57 species (see Simkanin *et al.*, 2005). Names corresponding to numbered field sites can be found in Table 1. Species sampled and their biogeographic affinities are found in Table 2.

Table 2. List of 57 species included in the present study. Biogeographic affinity of each species (N = 'Northern', S = 'Southern', B = 'Broadly-distributed' and I = 'Introduced') is also provided.

Species algae	Affinity/status	Species	Affinity/status
Codium spp.	B		
Laminaria hyperborea	N	Crustacea	
Laminaria digitata	B	*Chthamalus stellatus*	S
Saccharina latissima	N	*Chthamalus montagui*	S
Laminaria ochroleuca	S	*Semibalanus balanoides*	N
Alaria esculenta	N	*Balanus crenatus*	N
Himanthalia elongata	N	*Balanus perforatus*	S
Sargassum muticum	I	*Austrominius modestus*	I
Ascophyllum nodosum	N	*Campecopea hirsuta*	B
Pelvetia canaliculata	B	Mollusca	
Fucus spiralis	B	*Haliotis tuberculata*	S
Fucus vesiculosus	B	*Testudinalia testudinalis*	N
Fucus serratus	B	*Patella vulgata*	N
Fucus distichus	N	*Patella depressa*	S
Fucus indeterminate	B	*Patella ulyssiponensis*	S
Cystoseira spp.	S	*Gibbula umbilicalis*	S
Halidrys siliquosa	N	*Gibbula pennanti*	S
Bifurcaria bifurcata	S	*Gibbula cineraria*	B
Mastocarpus stellatus	N	*Phorcus lineatus*	S
Chondrus crispus	N	*Calliostoma zizyphinum*	B
Ascomycota		*Littorina littorea*	N
Lichina pygmaea	B	*Littorina saxatilis*	B
Porifera		*Melarhaphe neritoides*	B
Halichondria panicea	N	*Nucella lapillus*	N
Cnidaria		*Onchidella celtica*	S
Anemonia viridis	S	*Mytilus* spp.	B
Aulactinia verrucosa	S	Echinodermata	
Actina fragacea	S	*Asterias rubens*	B
Actinia equina	B	*Leptasterias muelleri*	N
Annelida		*Paracentrotus lividus*	S
Sabellaria alveolata	S	*Strongylocentrotus droebachiensis*	N
Sabellaria spinulosa	B	*Psammechinus miliaris*	B

width for every cluster number between 1 and 63. Large (maximal) values of the Mantel statistic or silhouette width, respectively, signal an optimum number of clusters. The rationale behind this choice becomes clear when recalling the fact that (i) the Mantel statistic measures the correlation between the pairwise distance matrix and the (equally sized) partition specific binary association matrix (0/1 for sites not/ belonging to the same cluster, respectively) while (ii) the silhouette width of a partition quantifies an average ratio of cluster separation and cluster size (between-cluster-distance/ within-cluster-distance). More details on these measures can be found in Borcard *et al.* (2011).

Eventually, the optimal number of clusters yields partitions which reflect groups of sites sharing:

(a) A similar ecological community (absence/presence) structure,
(b) Similar air (AT) and sea surface (SST) temperatures, or
(c) Similar wave height (WH) and Chl-a concentration.

Identification of key species

Given the optimal partition (a) with respect to community structure, the question arises how influential specific species are for the reconstructed groups. To address this question we employed the Indicator Value Index (Dufrêne & Legendre, 1997) which is a number $IndVal_{ij}$ computed for every combination of species i and group j. In short, the $IndVal_{ij}$ of Dufrêne and Legendre combines the aspects of *specificity* A_{ij}, i.e. the proportion of species i that is observed in group j, and *fidelity* B_{ij}, i.e. the proportion of sites in group j that are populated by species i. This takes the form of a product, i.e. $IndVal_{ij} = A_{ij}B_{ij}$. Since, as proportions, both A_{ij} and B_{ij} take values in the range between zero and one the same is true for the $IndVal_{ij}$. A value of one will result only if species i is present exclusively in group j and can be found at every site in this group. Notice that the IndVal value results from a combination of fidelity and specificity, so it is not resolved whether, e.g. a reduced IndVal value, is influenced most by fidelity, specificity or a combination of both.

Correlating community structure with environmental drivers

It is near at hand to correlate the partition resulting from (a) the community analyses with partitions (b) and (c) resulting from environmental factors (AT&SST) and (WH&Chl-a), respectively. This may be achieved by considering the adjusted Rand index that measures the (bias corrected) proportion of identical pairwise pairings, e.g. when a given pair of sites are assigned to the same groups in both community and environmental partitions (a) *vs* (b) and (a) *vs* (c). A value of unity can only be obtained for two identical partitions while zero/low values reflect the null-hypothesis of random partitions. In practice, we also visually inspected the partitions obtained and checked that results were in agreement with largest values of the adjusted Rand index.

All statistical analyses were carried out using R programming environment (R Development Core Team, 2008), including the 'kriging' package for interpolation of environmental data, as well as 'vegan', 'ade4' and 'cluster' for similarity index calculation and cluster analysis.

RESULTS

There was a strong positive Pearson correlation between SST and AT ($P = 0.009$, $r = 0.65$) and a statistically significant negative correlation between Chl-a and WH ($P = 0.03$, $r = -0.27$). None of the other combinations of parameters were significantly correlated with each other.

The averaged SST (2000–2003) for every site ranged from 9.76–13.6 °C and showed a clear differentiation between north-east and south-west (Figure 2A). The south-west was consistently ~2–3 °C warmer than the north-east of Ireland. There was a clear cut-off between a warmer area which stretched from Site 14 (Cangregga) in the west of Ireland up to Site 37 (Brownstown Head) in the south-east; and the cooler area between Site 54 (Rosstrevor) and Site 2 (Fanad Head) in the north-east. SST minima were recorded at Site 62 (Marconi's Cottage) and 54 (Rosstrevor). In addition, there were two central sectors of the Irish coast with

intermediate SSTs, one in the west from Site 13 (Black Head) to Site 3 (Bloody Foreland); and another in the south-east corner of the Irish Sea from Site 38 (Hook Head) to Site 53 (Port Oriel). Averaged ATs for every site showed similarities with the SSTs and the south-west was again warmer than the north-east (Figure 2B); however, AT minima were more extensive than in SSTs and reached from Site 4 (Rinnlea Point) in the north-west to Site 48 (Greystones) in the east. The extent of warmer AT sites was also extensive, stretching over the entire south-west of the country. There were two 'anomalous' areas of AT in the west, one of which was a cold area from Site 13 (Black Head) to 8 (Termoncarragh) and the second which was an anomalously warm area in the north-west between Site 7 (Easky) and Site 5 (Maghery-Termon). The latter cases broke an otherwise clear air temperature differentiation between south-west and north-east.

Chl-a values varied from 0 to 3.13 mg m^{-3} (Figure 2C). The overall averaged data (2000–2003) at every site showed low values in the north-west, west and parts of the central east. Chl-a was elevated in a sector of coastline in the south-east corner of Ireland between Site 35 (Helvick Head) and Site 47 (Ardmore Point). Apart from this sector, two other spots had high Chl-a; these were Site 9 (Dooagh Achill Island) and Site 52 (Balbriggan), along with a stretch of coastline on the north-east coast (in Northern Ireland). WH (Figure 2D) showed a marked differentiation between the south and east which was less exposed, and the north and west which was more exposed.

Marine community data

The distance matrix of marine community data based on the Sørensen index led to an optimal partition into two groups, based on both Mantel statistic and silhouette widths. Group 1 (●) dominated the north up to site 60 (Portmuck) and also dominated the west and south up to site 31 (Old Head of Kinsale). Meanwhile, Group 2 (●) dominated the East from site 32 (Gyleen) to 59 (Townhead) (Figure 3A). This clear east/west separation was only slightly marred by outliers of Group 1 in the south-east (sites 37, 38, 39) and of Group 2 in the west (sites 11, 12, 14, 20). Sites 12, 20 and 32, in particular, seemed not to fit well into their group, looking at silhouette results. They all belonged to Group 2 and were located at an 'outpost' area in the west. Corroboration of the Sørensen-based clustering scheme using an alternative distance metric (Raup–Crick) gave an almost identical partition of the marine community, suggesting that the partition was robust to metric choice (Supplementary Figure S1).

SST and AT

For temperature variables (which were positively correlated), the optimum number of groups by Mantel and silhouette calculations was four. Group 1 (●) dominated the south-west which was warmer than the rest of the coastline (Figure 3B; Figure 4A, B). Temperatures in the south-east and the north-east also clustered together (Group 4 ●) and this cluster was characterized by intermediate temperatures (Figure 4A, B); however there were several outlier sites in this sector of coast which were more associated with colder (Group 3 ●) or complex temperatures (Group 2 ●). Group 2 temperatures were considered 'complex' in the sense that, within this
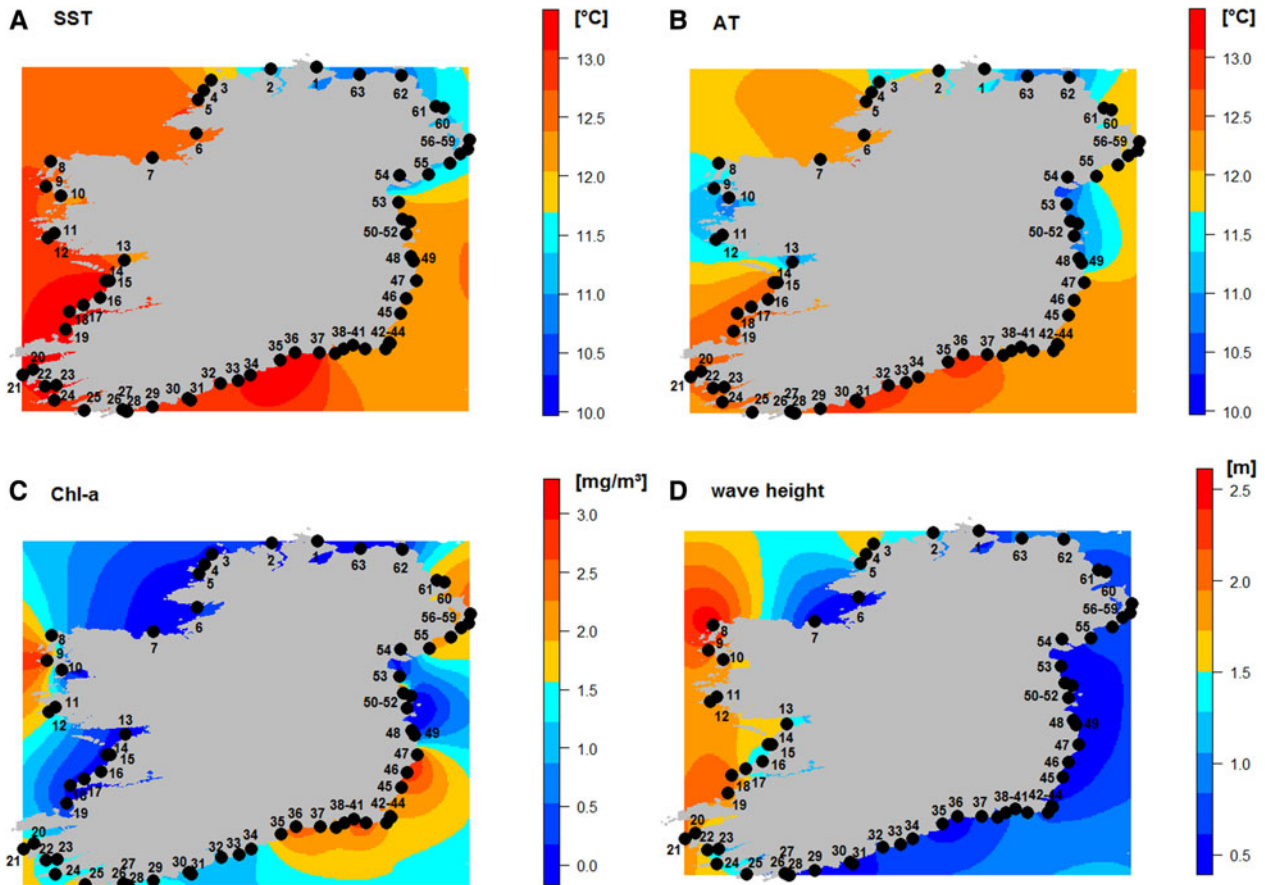
Fig. 2. Spatial distribution of environmental parameters (January 2000–December 2003 inclusive) on Ireland's coastline: (A) Mean Sea surface temperature (°C); (B) Mean Air temperature (°C), data for (A) and (B) were obtained from ICOADS; (C) Mean Chlorophyll-a (mg m^{-3}), data obtained from SeaWiFS; D) Mean Wave height (m), data obtained from Atlas of UK Marine Renewable Energy Resources & Wave Energy Resource Atlas Ireland.

grouping, median values of ATs were low while median SSTs were substantially higher (Figure 4A, B). Group 2 (●) was split across the central west and central east. Group 3 (●) had the lowest temperature values (Figure 4A, B); however there were only a few sites in this group, and these were all found in the north-east.

Chl-a and WH

These two parameters combined also clustered into an optimal partition of four groups (Figure 3C). This partition provided a clear differentiation between the east (Group 4 ●) and the west/north (mainly Group 1 ●), which aligned quite well with the community results (see below). Group 1 in the west and north was characterized by high WHs and low Chl-a; whereas Group 4 (east) was characterized by low values of both of these environmental factors (Figure 4C, D). There were some exceptional sites, e.g. a sector of the east coast with Group 1 conditions between Site 48 (Greystones) and 54 (Rosstrevor); but the overall pattern split between west and north *vs* the east, and most sites fell into one of these two groups. A minority of sites that fell into the remaining groups, i.e. Group 2 (●) and Group 3 (●) were reasonably widespread in the west; the latter had high Chl-a/low WH and the former had high values of both of these environmental factors (Figure 3).

Comparison of environmental data and species groupings

Adjusted Rand Index which is indicative of a match between the marine community and the environmental clusters, was highest (i.e. better match) for the Chl-a plus WH combination (AdjRand = 0.111), albeit these values were not statistically significant. But visual inspection showed a high overlap between the clustering partition based on Chl-a plus WH and the marine community groups, with a similar differentiation of east from west in each case. The margins between the east and western groups varied slightly between Chl-a plus WH and marine community partitions. In addition, there were exceptional sites in the east, which had different Chl-a plus WH conditions than the rest of this sector (see above), but this did not appear to influence the marine community pattern. Adjusted Rand Index values were lower for SST plus AT (AdjRand = 0.092, NS) and clusters formed from combined temperature variables were also not a good visual match for the community clustering pattern.

Species that contribute most to the marine community groupings

The results of the marine community grouping were analysed to distinguish species' contributions using the IndVal index. Only highly statistically significant IndVal values ($P = 0.01$
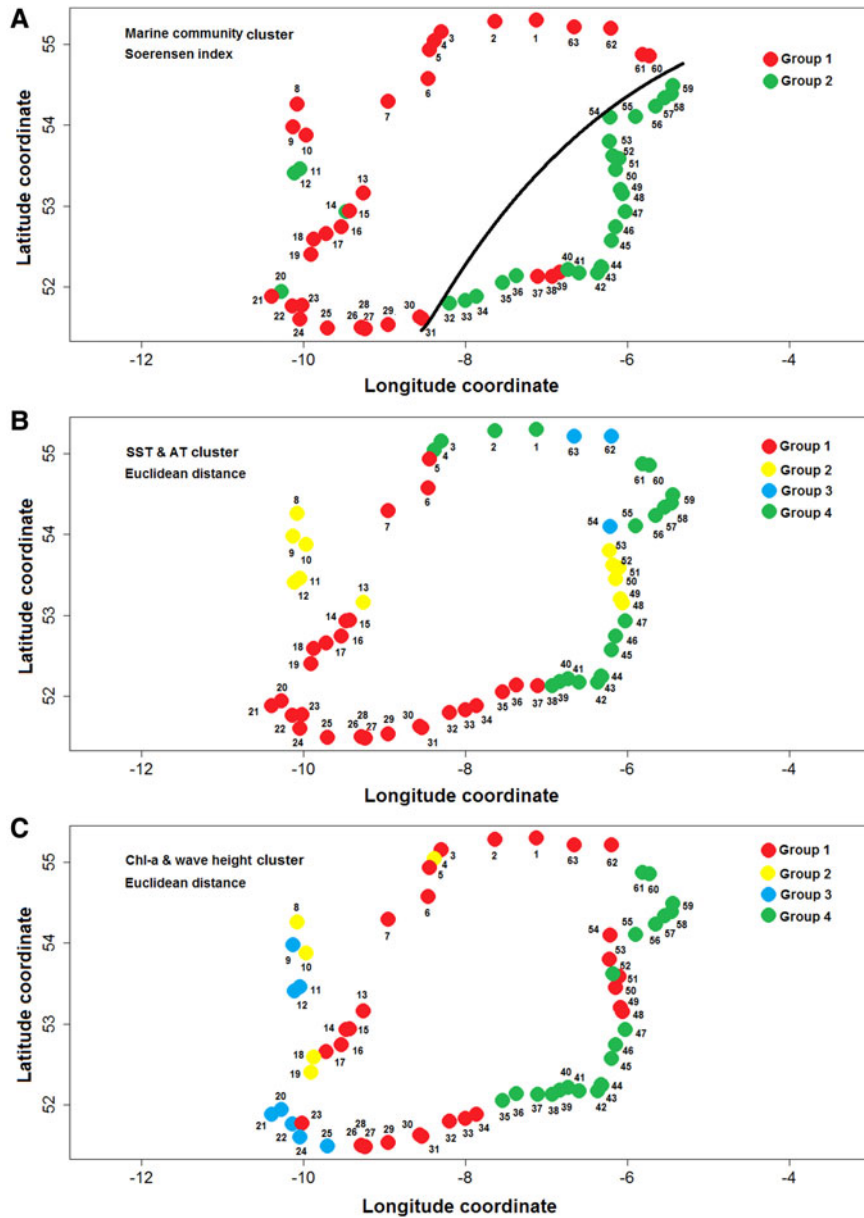
Fig. 3. Cluster results (complete linkage). The number of groups is based on analysis by Mantel statistic and calculating the optimum mean silhouette value: (A) Marine community data with two groups based on Sørensen's index, black line indicates partition trend; (B) Clustering of the combined parameters Sea surface temperature (SST) and Air temperature (AT) based on Euclidean distance; (C) Clustering of the combined parameters Chlorophyll-a (Chl-a) and wave height based on Euclidean distance.

or lower) were considered, in order to emphasize the most important species contributing significantly to a group, and also the most important ones to differentiate between the groups (Table 3). The western Group (●) was highly influenced by the sea urchin *Paracentrotus lividus* (Figure 5A) and the green algae *Codium* spp. (Figure 5F). In addition, species such as the lichen *Lichina pygmea*, the brown alga *Himanthalia elongata* (Figure 5B), the barnacle *Chthamalus stellatus* (Figure 5C), the sea snails *Melarhaphe neritoides* (Figure 5D), *Patella ulyssiponensis, Actinia equina* and *Alaria esculenta* (Figure 5E) were also important for western communities. For the eastern cluster (●), the most influential species were the barnacles *Balanus crenatus* (Figure 5G) and *Austrominius modestus* (Figure 5H) as well as the algae *Fucus vesiculosus*.

DISCUSSION

This study shows that it was possible to discern spatially coherent groupings in the rocky intertidal community on Irish shores. The community sampled comprised a combination of species which are 'indicators' of global warming, along with 'broadly-distributed' taxa (Laffoley *et al.*, 2005; Simkanin *et al.*, 2005; see Table 2), some of which may interact biologically with the former groups. The Sørensen index, using just presence/absence of species identified two large groups; one dominant community in the Irish Sea and southeast (termed 'east') and a second dominant community in the south-west, west and north (termed 'west'). The complete linkage method, which is the most conservative way of clustering, was used to obtain these groups. Less conservative
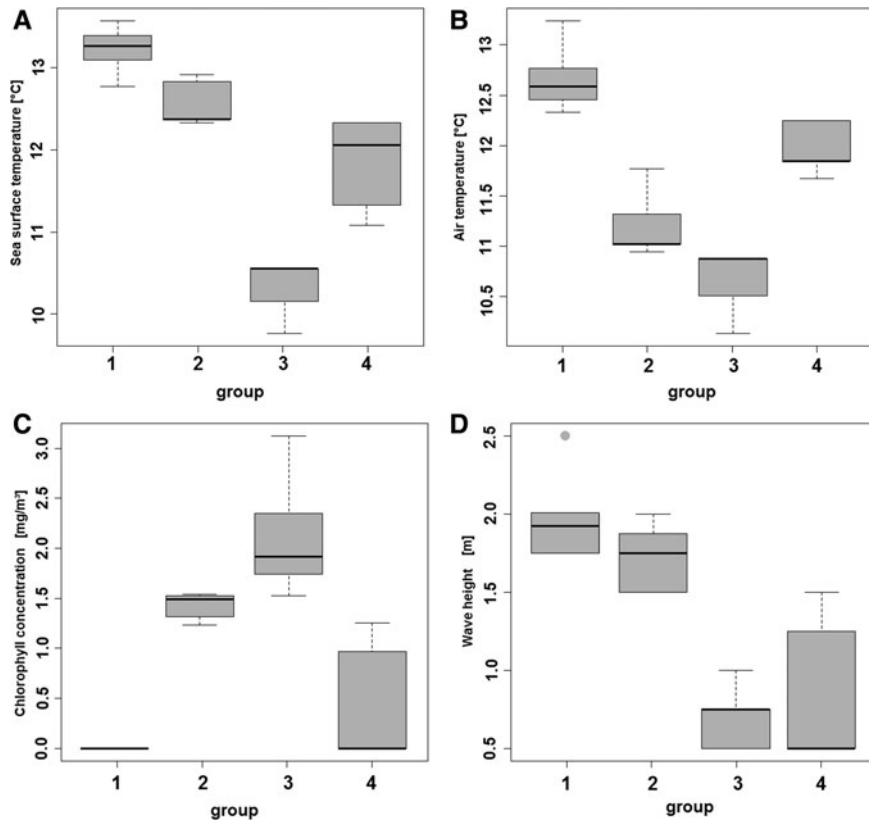
Fig. 4. Boxplots (black line indicates median) for the values of the four environmental parameters based on grouping of sites shown in Figure 3 (A) Sea surface Temperature, (B) Air temperature, (C) Chlorophyll-a and (D) Wave height.

Table 3. Species contribution to the two different groups found by Sørensen's index and using IndVal index (highly significant species, i.e. $P = 0.01$ or lower, are presented in bold).

| Group 1				Group 2			
Species	**Area**	**IndVal**	**P-value**	**Species**	**Area**	**IndVal**	**P-value**
Codium spp.	**west**	**0.577**	**0.001**	Laminaria hyperborea	east	0.294	0.026
Laminaria digitata	west	0.561	0.080	Saccharina latissima	east	0.455	0.070
Alaria esculenta	**west**	**0.470**	**0.001**	Ascophyllum nodosum	east	0.386	0.069
Himanthalia elongata	**west**	**0.773**	**0.001**	Pelvetia canaliculata	east	0.391	0.991
Fucus indeterminate	west	0.137	0.952	Fucus spiralis	east	0.437	0.403
Cystoseira spp.	west	0.148	0.089	**Fucus vesiculosus**	**east**	**0.609**	**0.001**
Halidrys siliquosa	west	0.465	0.071	Fucus serratus	east	0.525	0.065
Bifurcaria bifurcata	west	0.205	0.023	Mastocarpus stellatus	east	0.457	0.921
Chondrus crispus	west	0.476	0.838	Anemonia viridis	east	0.277	0.751
Lichina pygmaea	**west**	**0.554**	**0.004**	Actinia fragacea	east	0.206	0.099
Halichondria panicea	west	0.471	0.199	Sabellaria alveolata	east	0.123	0.228
Aulactinia verrucosa	west	0.185	0.306	Semibalanus balanoides	east	0.497	0.858
Actinia equina	**west**	**0.553**	**0.001**	**Balanus crenatus**	**east**	**0.481**	**0.002**
Chthamalus stellatus	**west**	**0.706**	**0.001**	**Austrominius modestus**	**east**	**0.696**	**0.001**
Chthamalus montagui	west	0.541	0.065	Testudinalia testudinalis	east	0.103	0.111
Patella vulgata	west	0.502	0.860	Phorcus lineatus	east	0.367	0.596
P. ulyssiponensis	**west**	**0.592**	**0.003**	Littorina littorea	east	0.513	0.123
Gibbula umbilicalis	west	0.492	0.389	Asterias rubens	east	0.311	0.888
Gibbula cineraria	west	0.472	0.231				
Calliostoma zizyphinum	west	0.325	0.060				
Littorina saxatilis	west	0.503	0.206				
Melarhaphe neritoides	**west**	**0.773**	**0.001**				
Nucella lapillus	west	0.505	0.626				
Mytilus spp.	west	0.525	0.226				
Paracentrotus lividus	**west**	**0.500**	**0.001**				
Psammechinus miliaris	west	0.128	0.181				
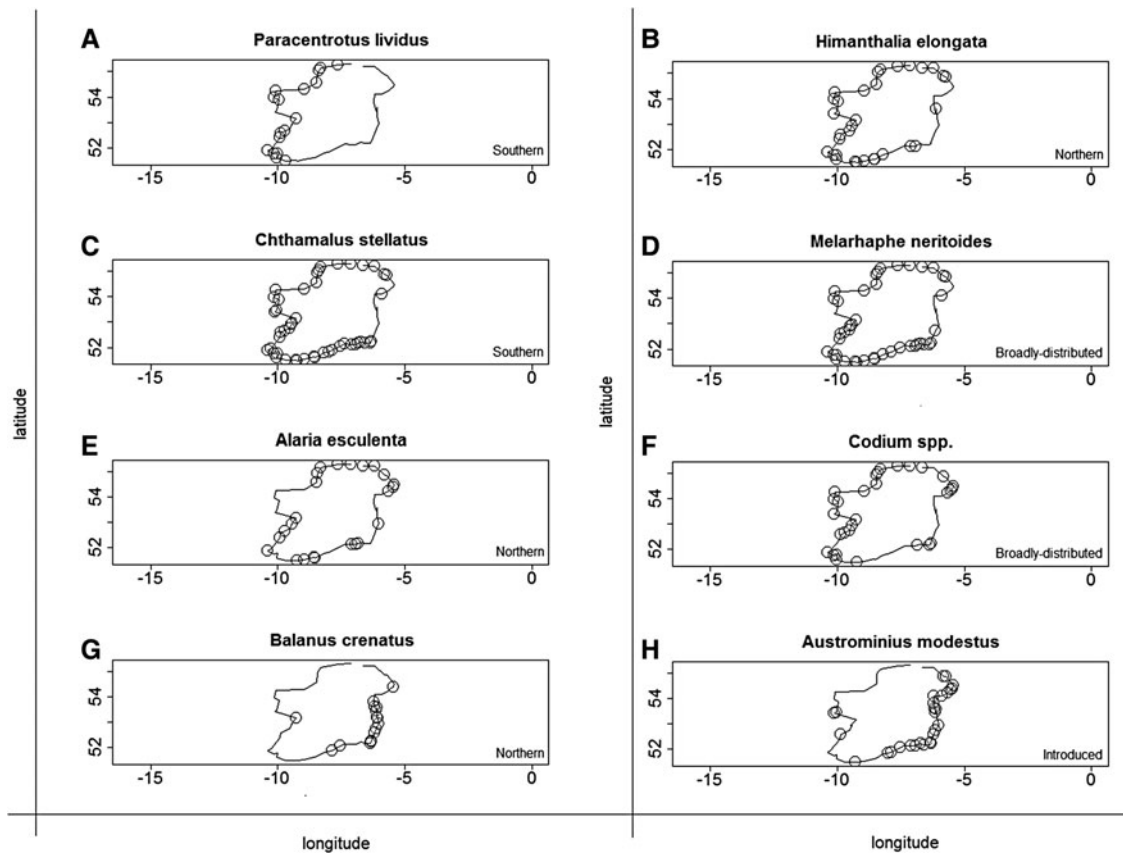
Fig. 5. Distributions for selected species contributing to their respective group using Sørensen's index (A–F = west; G–H = east), (A) *Paracentrotus lividus*, (B) *Himanthalia elongata*, (C) *Chthamalus stellatus*, (D) *Melarhaphe neritoides*, (E) *Alaria esculenta*, (F) *Codium* spp., (G) *Balanus crenatus*, (H) *Austrominius modestus*. Biogeographic affinity of each species ('Northern', 'Southern', 'Broadly-distributed' and 'Introduced') is also provided.

methods of clustering (Ward/single linkage) or alternative routes to selecting optimal numbers of groups might have tweaked this pattern, but these are unlikely to have led to another community pattern that differed markedly from the 'east' *vs* 'west' groupings that were observed here. Also, a separate analysis using the Raup–Crick distance metric gave almost identical results. Although 'biotopes' have been mapped previously (e.g. Costello *et al.*, 1996), defining the marine communities on different parts of the Irish coast has not been carried out before and the present study is novel in this respect.

Establishing the degree to which the detected groups were related to environmental factors was a follow-on objective. Before addressing this, correlations between the environmental parameters were investigated. Unsurprisingly, there was a highly significant positive correlation between both temperature variables. Temperature data showed a broadly latitudinal trend, with higher temperatures in the south-west and lower values in the north-east, and intermediate values or more complex combinations separating these 'warm' and 'cold' sectors of coastline. Meanwhile, a significant negative correlation was found between Chl-a and WH, indicating that exposed shores tended to be associated with lower Chl-a. High flushing rates at exposed sites may have led to lower accumulated microalgae in these locations (Kraufvelin *et al.*, 2002). Wave height was lower in the east, as this part of the coast is more sheltered from prevailing south-westerly winds (Sweeney, 2014). But, while Chl-a was generally low in the east, certain south-eastern sites showed the highest values

nationally. Such 'local' variability arises because the south-east corner of Ireland is the location of the well-known Celtic Boundary Front, which is associated with seasonally elevated primary productivity (McGinty *et al.*, 2014). This south-east corner is also the location of a large shallow delta where some of Ireland's largest rivers (rivers Suir, Nore and Barrow) empty into the sea, which would also have contributed to locally elevated nutrients along the south-east coast.

Cluster analysis of the standardized environmental data using complete linkage and Euclidean distance led to an optimum of four groups for the combined parameters (Chl-a & WH), as well as for the combined temperature parameters (SST & AT). However, the marine community did not reflect the cluster pattern in temperatures, despite the fact that the assemblage included many warm- and cold-adapted species. It was clear that mean temperature clusters, which were more north/south in orientation, were at odds with the east/west spatial pattern in marine community groups. For example, 'complex' group 2 temperatures occurred in the central east and central west coast, and this was at odds with the east/west community pattern. 'Complex' temperature groups were so-called because of simultaneously high SSTs and low ATs. Conditions at these central sites also contrasted strongly with an otherwise general pattern of warmer temperatures in the south-west and cooler temperatures in the north-east. For simplicity, only clustering based on mean temperatures has been presented, however repeating this exercise based on temperature maxima and minima did not improve the spatial match between temperature variables and the

marine community. Research has shown that marine community structure may be affected by subtle environmental signals such as temporal variability in oceanographic variables (Wieters *et al.*, 2009), especially in areas with coastal wind-driven upwelling. Despite the lack of an overall community association with temperature in the present study, the distribution of individual species was likely to have been associated with it, e.g. *Testudinalia testudinalis* which was restricted to the colder north-east. Intertidal *Balanus crenatus* was also restricted to the east; this is a low shore specialist and is known to be intolerant of the higher temperatures that could result from heating up of the substrate by insolation at low tide (Southward, 1958). Similarly, 'southern' species, like *Phorcus lineatus*, were generally restricted to the southern half of the country.

Unlike temperature, there was a reasonably high visual similarity between the clustering patterns in the marine community and the Chl-a plus WH data. The group 2 marine community in the east and south-east was associated with smaller waves and lower Chl-a, albeit with local exceptions to this trend, e.g. high Chl-a in the south-east corner, as previously discussed. On Ireland's western shores, three different WH and Chl-a combinations were found; these approximately corresponded to the group 1 marine community cluster in the west. The west community mainly had the same spatial arrangement as high levels of wave exposure and low levels of Chl-a. Again, local variability within this overall trend occurred, i.e. sites with reduced WH and elevated Chl-a; this was due to locally sheltered bays along the west coast. In some cases, these shores corresponded to exceptional cases of marine community group 2 along the west coast (e.g. sites 11, 12 and 20), strengthening the evidence that these environmental parameters were important community drivers.

In general, the results of the present study agree with others which demonstrated that wave exposure has a strong structuring role in marine communities. A study in Scotland showed that wave fetch was an important predictor of rocky intertidal community patterns (Burrows *et al.*, 2008). The explanatory power of wave fetch in that case was highest at very fine local scales, and this reduced at scales >10 km (Burrows *et al.*, 2008). Other studies have shown links between wave exposure and the biomass of dominant species (McQuaid & Branch, 1984). Chlorophyll-a is also a good predictor of marine subtidal communities, e.g. this may be associated with the abundance of micrograzers (Burrows, 2012). Indirect effects on intertidal species diversity in association with primary production have also been shown (Burrows *et al.*, 2008).

Looking at the species determining the two marine community groups, an IndVal index (Dufrêne & Legendre, 1997) was used as an alternative to the SIMPER routine in the PRIMER program. The latter is widely used but is restricted to the Bray–Curtis similarity metric and hence not suitable for the present case (Clarke & Warwick, 2001). For the western marine community group, the IndVal index showed that the species *Paracentrotus lividus*, *Lichina pygmea*, *Codium* spp., *Himanthalia elongata*, *Chthamalus stellatus*, *Melarhaphe neritoides*, *Patella ulyssiponensis*, *Actinia equina* and *Alaria esculenta* played big roles. Some of these species can clearly be related to high wave exposure and thus reflected the environmental data very well. For example, the presence of species such as *A. esculenta*, *H. elongata*, *C. stellatus*, *P. ulyssiponensis* (formerly 'aspera') and

Melarhaphe (formerly 'Littorina') *neritoides* are associated with elevated wave exposure (Ballantine, 1961). Also at exposed shores, *C. stellatus* tends to be more abundant than other barnacles (*C. montagui*) in the juvenile phases, where it prefers wetter conditions (Power *et al.*, 2001, 2006; Delany *et al.*, 2003). Why the sea urchin *P. lividus* and green alga(e) *Codium* spp. are indicators for the west is not easily explained; but these species also mainly occur on the west coast of Britain (Pizzolla, 2007) and an environmental explanation for this seems likely.

For the eastern group, the species *Balanus crenatus*, *Austrominius modestus* and *Fucus vesiculosus* were indicators. The abundance of *A. modestus* is higher on sheltered coasts in Ireland (Allen *et al.*, 2006), which agrees with trends already noted above. Though it was not identified by the IndVal, the edible periwinkle *Littorina littorea* was also associated with 'east' coast communities in the present study, a fact which may have links to enriched conditions. In addition to *L. littorea*, several other harvested species were also associated with the eastern group (*Laminaria hyperborea* and *Ascophyllum nodosum*), albeit not significantly so. Interestingly, the barnacles *C. stellatus*, *B. crenatus* and *A. modestus* seemed to have mutually exclusive distributions over the island; *C. stellatus* strictly prevailed in the west while the other two were very widespread in the east (Figure 5). As *A. modestus* is an invasive species, its introduction in the east was almost certainly associated with closer proximity to many shipping routes along this coast, or more speculatively, with occupation of empty niche space due to the relatively low presence of *C. stellatus* in the east. Overall diversity of species contributing to the 'western' group was higher (N = 26 species) than the eastern one (N = 18; Table 3), however, it should be emphasized that 'presence' or 'absence' is effort-dependent; in this case, representative of a search effort of approximately 2 person-hours searching for 57 species per site.

Four years of environmental data is probably adequate for looking at community structure at a single point in time, since this equates with turnover rates for many intertidal species; although some species (like upper shore barnacles) may live for much longer than this (Southward, 1991; Lewis, 1996). Local anthropogenic impacts could also have a reasonable effect on community structure, although these were expected to occur at point-locations in association with patterns of human settlement around the coastal cities. Overall, the large groupings on the east *vs* the other coasts make it unlikely that the explanations for community assemblages were due to local anthropogenic effects, or indeed, due to stochastic processes. As the marine community data was collected over one year (2003) by the same set of operators at all sites, the impact of operator errors at the sites was removed.

CONCLUSIONS

There was no clear signal in the intertidal community relating to mean sea or air temperature. This was interesting, given the mixture of warm- and cold-adapted species in the sampled community, the fact that temperatures varied markedly different along the coast, and the knowledge that individual marine populations undoubtedly respond to temperature (Sunday *et al.*, 2012). Temperature variables presented a largely latitudinal trend, whereas there was a longitudinal (east/west) trend

in community composition. Intertidal community groups presented a similar spatial arrangement to combined wave exposure and Chl-a and the habitat preferences of several species which characterized community groups reflected wave exposure preferences very well. This study is intended to illustrate how attempts to monitor impacts of global warming on the marine intertidal community may be frustrated by local processes (Chl-a and wave height varied locally as well at the scale of broader coastline). The study may also inform future monitoring of harvesting and indirect effects of such practices on intertidal community composition, e.g. species richness was lower in the east, but this community included several harvested species (*L. littorea* and, to lesser extent, *L. hyperborea* and *A. nodosum*).

SUPPLEMENTARY MATERIAL

ACKNOWLEDGEMENTS

FINANCIAL SUPPORT

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