Biological Zonation and Bedrock Strength on a High Energy Granite Shore Platform

Authors: Burningham, Helene, and Knight, Jasper

Source: Journal of Coastal Research, 95(sp1) : 23-28

Published By: Coastal Education and Research Foundation

URL: https://doi.org/10.2112/SI95-005.1

Journal of Coastal Research	SI	95	23–28	Coconut Creek, Florida	2020

Biological Zonation and Bedrock Strength on a High Energy Granite Shore Platform

Helene Burningham[†*] **and Jasper Knight**[‡]

[†]Department of Geography
University College London (UCL)
London, UK

[‡]School of Geography, Archaeology and Environmental Studies
University of the Witwatersrand
Johannesburg, South Africa

www.cerf-jcr.org

www.JCRonline.org

ABSTRACT

Burningham, H. and Knight, J. 2020. Biological zonation and bedrock strength on a high energy granite shore platform. *In:* Malvárez, G. and Navas, F. (eds.), *Global Coastal Issues of 2020*. *Journal of Coastal Research*, Special Issue No. 95, pp. 23-28. Coconut Creek (Florida), ISSN 0749-0208.

Many studies have shown that downwearing of rock shore platforms results from interactions between biological and geomorphological processes, but the relative roles of biological, lithological and external (wave hydraulic action) in shaping rock shore platforms have not been examined in detail. This is important, however, because surface organisms can both increase and decrease rates of platform downwearing by biological weathering and bioprotection, respectively. This study presents biological and geomorphological results from a high energy shoreline in northwest Ireland. Here, the 50-100 m wide granite shore platform has a slope of ~1:6 and extends from 7-9 m above the level of mean high water springs to ~2 m below mean low water. Organisms attached to the bedrock surface were surveyed by the quadrat method along two shore-normal topographic transects. At each quadrat site, bedrock hardness was measured using an Equotip instrument. Results show clear ecological zonation that can be directly related to the tidal frame. There is very little evidence for cross-shore changes in bedrock hardness. Elevation is the most significant driving factor for the presence of different species, but bedrock hardness is only associated with the abundance of specific species such as barnacles, demonstrating complexity in biogeomorphological relationships at local scales.

ADDITIONAL INDEX WORDS: *Algae, bedrock hardness, Ireland, lichen, rock coast, shore platform.*

INTRODUCTION

Rocky shoreline ecosystems are significant areas of high biodiversity globally (Fenberg and Rivadeneira, 2019; Silliman *et al*., 2011) and are also significant because of the role of rocky coasts in mediating the effects of ongoing climate change, storms and sea-level rise (Harley and Helmuth, 2003; Jackson and McIlvenny, 2011). The physical properties and ecosystems of rocky shorelines are closely linked to the nature of the bedrock surface and other geological properties such as bedrock structure and geochemistry (Ramos *et al*., 2016; Wilding *et al*., 2010). Several studies have described the biological zonation of lichen, algae and other organisms such as barnacles across rock platforms, demonstrating a clear and genetic relationship between position in the tidal frame and different biological assemblages (Chappuis *et al*., 2014; Konar *et al*., 2009; Munroe and Noda, 2009; Sheard, 1968). Despite this intuitive relationship to the bedrock substrate, few studies have explored the detailed relationship between rock surface ecosystems and the nature of the rock surface itself. For example, Stafford *et al*. (2015) showed that rock surface aspect and microtopography influence the microclimate that in turn controls physiological stress of surface ecosystems. Ramos *et al*. (2016) used multivariable analysis and logistic regression to show how coastal geomorphology, aspect and lithology control distinctive macroalgae communities on the exposed rock coasts of northern Spain. Several studies have also examined the ecology of rocky shorelines around the UK and Ireland (Blight *et al*., 2009; Burrows *et al*., 2002; Davenport and Davenport, 2005; Firth and Crowe, 2008, 2010; Healy, 1996; Jackson and McIlvenny, 2011; O'Connor, 2010), but these have focused on the description of species assemblages and not their link to substrate properties.

The aim of this study is to describe the relationship between shore platform biological zonation and the physical properties of the platform, in particular bedrock strength. The motivation behind this study is that rocky shore organisms have the potential to decrease bedrock strength (by bioweathering) and to increase bedrock strength (by bioprotection). The interplay between these different potential outcomes has not been explored in detail (Coombes *et al*., 2013). This study contributes to this debate by presenting detailed field evidence for rock surface ecosystems and hardness values from a study site in northwest Ireland.

STUDY AREA

Rocky shorelines are common in northwest Ireland, influenced by the presence of hard granite bedrock and high-energy wave and macrotidal regimes that result in high rates of abrasion and shoreline change (Thébaudeau *et al*., 2013). Several studies highlight the role of bedrock geology and structure on contemporary coastal features (Burningham, 2008; Cooper, 2006). Northwest Ireland was also strongly affected by Quaternary glacial erosion and sea-level change, and thus can be classified as a paraglacial coastline (Knight and Harrison, 2018). Although

DOI: 10.2112/SI95-005.1 received 31 March 2019; accepted in revision 13 February 2020.
*Corresponding author: h.burningham@ucl.ac.uk

many coastal elements can be considered as relict paraglacial features (Knight and Burningham, 2014, 2015), there is less understanding of contemporary processes along rocky coasts and their controls (Cullen and Bourke, 2018; Knight and Burningham, 2011). The Atlantic-facing granite rock platform on the north shoreline of Gweebarra Bay (between Trawenagh and Falchorrib: Figure 1) has been examined with respect to boulder dynamics (Knight and Burningham, 2011) but these shorelines also contain diverse ecosystems existing on bedrock surfaces (Sheard, 1968). In detail, Trawenagh Bay is underlain by Dalradian-age biotite granite (Long and McConnell, 1999) and has a mesotidal regime (1.6 m neap and 3.5 m spring tidal range) with mean annual offshore wave height of 2.9 m. The rock shoreline under study is 1.2 km long and faces southwest towards the open Atlantic.

METHODS

Biological organisms attached to the shore platform surface were surveyed within 50x50 cm quadrats along 4 transects, two covering the immediate supra- (to ~6.5 m above mean sea level (MSL)) and intertidal platform to around mean low water neaps (*i* and *ii* in Fig. 1), and the other two the higher (6.0-10.5 m above MSL) supratidal (*iii* and *iv* in Fig. 1). Sampling sites were spaced at 3-5 m intervals along the transects and specifically avoided rock pools. Species presence and % abundance was recorded in each quadrat, as was bedrock surface hardness using an Equotip instrument. This instrument has been previously used on similar dry, smooth coastal bedrock surfaces (Knight and Burningham, 2019; Viles *et al*., 2011). At each point, 50 surface rebound measurements were taken (n=1700 in total), avoiding bedrock structures, areas of surface flaking, and obscuring vegetation growth. Both species' relationships and Equotip values were then examined quantitatively using standard methods. Sample sites were positioned using a dGPS with ±3 cm accuracy. Shore platform topography was acquired during a separate UAS survey of the site using dGPS defined ground control points for 3D control. Structure-from-motion photogrammetry (Smith *et al.*, 2016) was undertaken and used to generate a DSM at 0.1 m spatial resolution, with a 3D RMSE of 0.05 m; topographic profiles were extracted for the surveyed transects.

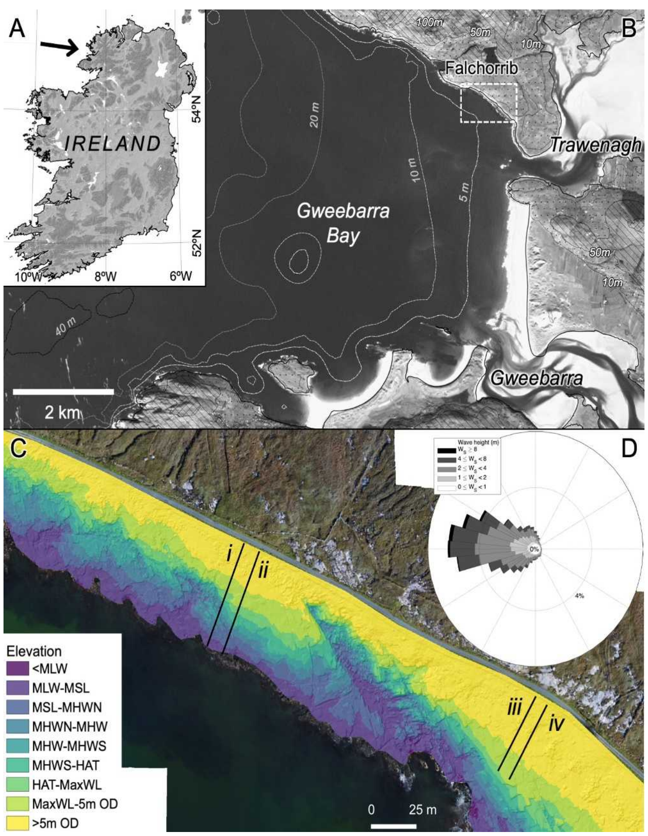

Figure 1. (A) Location of study site in northwest Ireland, (B) detailed location of Gweebarra Bay and the Falchorrib-Trawenagh shoreline, (C) the shore platform digital surface model and transect positions i-ii and iii-iv, and (D) the offshore wave rose.

RESULTS

Bedrock Surface Hardness

Equotip values are plotted according to distance, and thus position in the tidal frame, along transects *i*-*ii* and *iii*-*iv* (Figures. 2A, 3A). Results from all transects show that the shore platform has a relatively uniform slope of ~1:6 that does not show any significant change in angle at different elevations above and

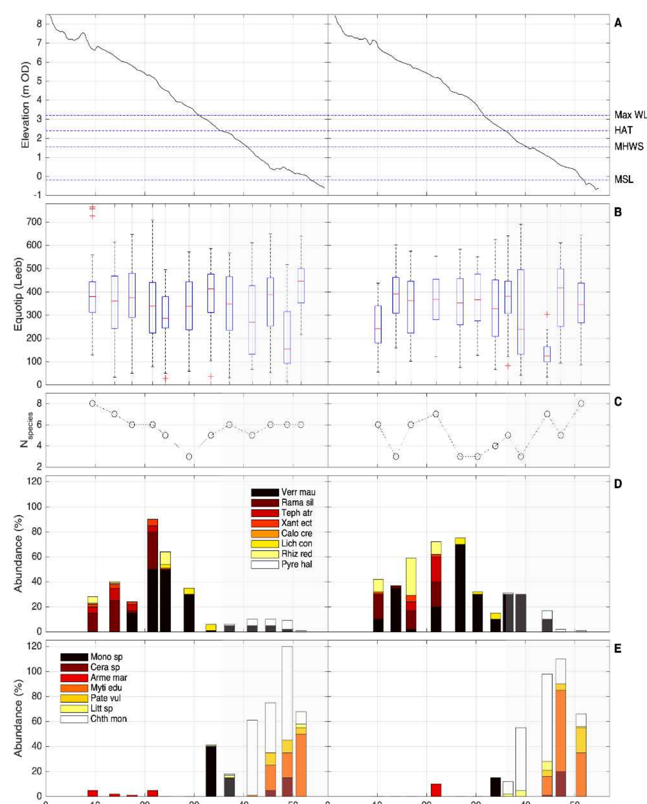

Figure 2. Topographic profiles (A) along transects *i* (left) and *ii* (right), showing Equotip hardness values (B), species richness (C), lichen (D) and other (E) species abundance for key taxa (lichen - *Verrucaria maura, Ramalina siliquosa, Tephromela atra, Xanthoria ectaneoides, Caloplaca crenularia, Lichina confinis, Rhizocarpon reductum., Pyrenocollema halodytes*; seaweed - *Monostroma sp., Ceramium sp.*; plants - *Armeria maritima*; and animals - *Mytilus edulis, Patella vulgata, Littorina sp., Chthamalus montagui)*. Shaded zone on panels B-E highlights the intertidal zone.

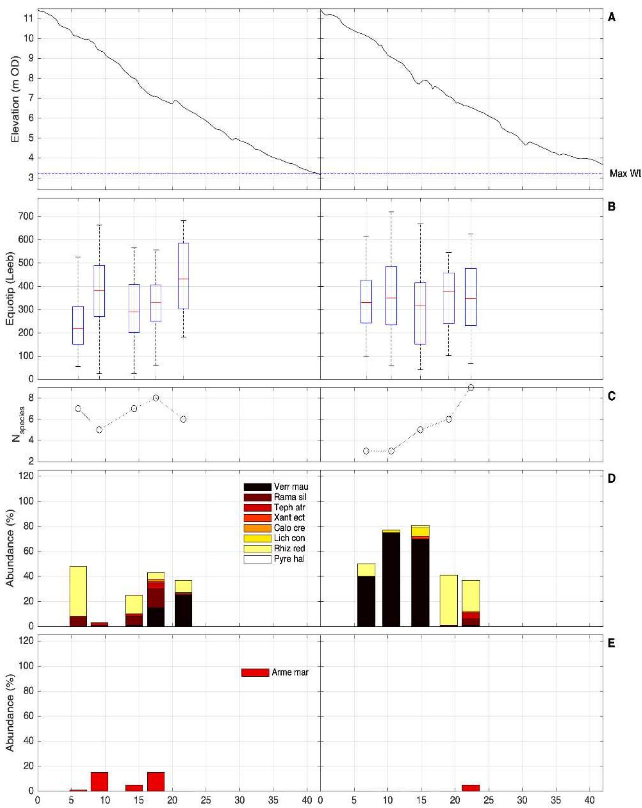

Figure 3. Topographic profiles (A) along transects *iii* (left) and *iv* (right), showing Equotip hardness values (B), species richness (C) and lichen (D) species abundance for the taxa listed in Fig. 3.

below the intertidal zone. Slight variations in the profile can be attributed to structural control on the disposition of the granite bedrock surface (Figure 4).

In detail, Equotip rebound values along the transects show remarkably similar values but with large variance in repeat measures at each site (Figures 2B, 3B). Although variability between adjacent points is evident, no systematic patterns can be identified with respect to the positions of highest astronomical tide (HAT) or mean high water springs (MHWS). The median rebound Leeb value for the supratidal zone of *i/ii* (within about 4 m of the maximum tide level (Max WL)) was 353, compared with 323 in the intertidal zone; but at *iii/iv*, the higher supratidal zone had a median was 316. At the 99% confidence level, there was a significant difference in Equotip rebound values between the inter- and low supratidal zones (χ=8.2, p<0.01), but not between low and high supratidal (χ=3.78, p=0.052) or inter- and high supratidal (χ=1.08, p=0.3). This suggests that the hardness of the low supratidal zone is distinctly greater than that of the more seaward or landward surfaces.

Species Diversity and Spatial Patterns

Ecological results for the transects are shown in Figures 2C-E (*i-ii*) and 3C, D (*iii-iv*). In terms of overall species diversity, both sites show similar and uniform patterns with 6-8 species commonly recorded. Across transects *i-ii*, there is a clear transition in lichen, plant, seaweed, and animal assemblages between the supra- and intertidal zones (Figure 2D, E). Some species such as the supratidal lichen *Ramalina siliquosa* or intertidal mussel *Mytilus edulis* are only present in specific zones, whereas the lichen *Verrucaria maura* is more prolific (Figure 4C) and present across a wide band above and below the high water shoreline. Individual species reach up to 60% abundance per quadrat, which is particularly notable where *V. maura* or the barnacle *Chthamalus montagui* dominate the platform surface. Across the high supratidal zone (transects *iii-iv*), the coastal plant *Armeria maritima* is commonly found occupying discrete depressions or fractures in the rock surface. Overall, there is a clear zonation of species relative to a land-sea, topographic gradient, but that marine species perhaps occupy a broader vertical range here than the tidal frame (as defined by tide observations at the Aranmore gauge, ~12 km northwest of the site) would otherwise define.

Figure 4. Physical properties of the Falchorrib-Trawenagh shoreline. (A, B) Bedrock structures giving rise to variations in granite surface topography, (C) different lichen species covering the rock surface, (D) granite surface weathering features.

Cross-correlation between different biological and physical properties of the shore platform surface shows some statistically significant positive and negative correlations (Figure 5). There are positive and co-dependent relationships between the lower intertidal animal and seaweed species *M. edulis*, *Patella vulgata* (limpet), *Chthamalus montagui* (barnacle), *Littorina* sp. (periwinkle) and *Ceramium* sp. (red algae) which all exhibit negative (albeit weak) correlations with the green algae *Monostroma* sp. Most lichen species are also negatively correlated with these intertidal creatures due to their mutual separation across the tidal frame, however the marine lichen *Pyrenocollema halodytes* is strongly correlated with *C. montagui* as both are specifically found lower in the tidal frame. Lichen species are variably correlated; *Ramalina siliquosa* (a fruticose lichen) and *Xanthoria ectaneoides* (a foliose lichen) show the strongest positive relationship, and are both common coastal lichen found on siliceous rocks as is *Tephromela atra* (a crustose lichen).

Of the physical factors examined, elevation is positively related to several lichen species, but most significantly to *Rhizocarpon reductum* (a crustose lichen commonly found on siliceous rocks) which clearly prefers the higher elevations. Elevation is negatively correlated with *P. halodytes*, a species of lichen that prefers calcareous surfaces, and here on a granite (siliceous) platform

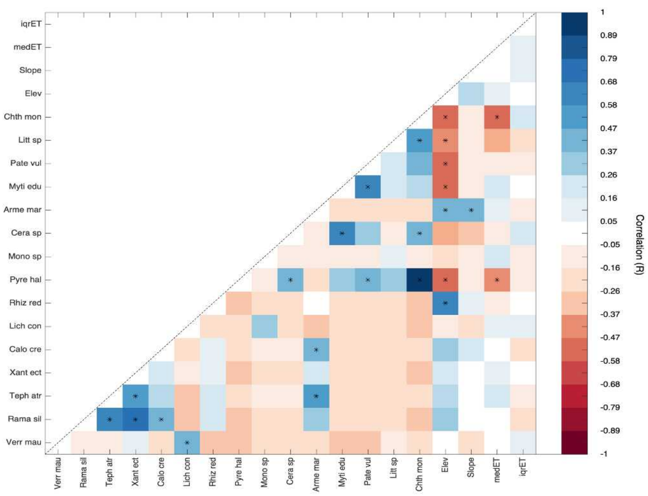

Figure 5. Cross-correlation between biological (abundance of the key species referred to in Fig. 3) and physical properties (slope, elevation, median and interquartile range in Equotip value) of the shore platform [* indicates correlations that are significant at the 99% confidence level].

occupies the surfaces of shell organisms such as *C. montagui* and both are found low in the tidal frame. Elevation is significantly positively correlated with *A. maritima*, the coastal plant found in the higher supratidal zone, and significantly negatively correlated with the marine animals *M. edulis, P. vulgata, Littorina* sp. and *C. montagui*.

C. montagui and *P. halodytes* are the only biological organisms to show a significant (in this case, negative) relationship to Equotip values; specifically that surfaces with increased abundance of these species have lower Equotip rebound values and surfaces with decreased abundance have higher rebound values. Neither bedrock hardness nor local variance in hardness are specifically correlated with either elevation of platform surface slope.

DISCUSSION

This study shows that covariability between different rocky shoreline species, and between individual species and rock surface properties, is highly variable (Figure 5). Based on species composition within individual quadrats (Figures 2D, E, 3D), most species do not show significant relationships or co-dependencies, suggesting that they do not occupy narrow environmental niches. *C. montagui* and *P. halodytes* are an exception to this in that the marine lichen *P. halodytes* has a specific preference for calcareous surfaces that, in siliceous coastal rock environments, are only found on the shells of marine organisms. Individual species only appear to dominate at certain topographic positions, such as the barnacle *C. montagui* on the upper foreshore, and the black lichen *V. maura* within the wave splash zone. This is consistent with previous studies where individual species occupy a relatively wide elevational range (Sheard, 1968). Elevation range is likely expanded on exposed coastlines due to the potential reach of wave runup and splash. Many studies show that species assemblages are strongly controlled by elevation, determining inundation/exposure period and microclimate (*e.g.*, Chappuis *et al*., 2014; Davenport and Davenport, 2005; Harley and Helmuth, 2003; Sorte *et al*., 2019). These environmental stresses are also influenced by site-specific factors of wave exposure and thus coastal aspect (Lindegarth and Gamfeldt, 2005; Ramos *et al*., 2016; Stafford *et al*., 2015), and microscale variations in shoreline topography and weathering patterns (Firth and Crowe, 2010). Although results suggest that species diversity tends to increase with elevation, with lower concomitant dominance by any one species (Figures 2, 3), there is no significant difference in richness between zones or correlation with elevation. The biological associations here suggest some complexity in relationships between species and environment. Martins *et al.* (2008) and Konar *et al*. (2009) found statistical relationships between lower elevation but not higher elevation species, and increasing ecosystem patchiness with increased elevation. External environmental controls and intrinsic ecosystem dynamics can thus drive complex patterns and scale-dependency in rock shoreline ecosystems (Underwood and Chapman, 1998).

Rock surface hardness can help inform on the interactions between these external and intrinsic controls. Several previous studies show how mechanical erosion by waves can remove a weathered rock carapace, exposing harder rocks beneath (Matsumoto *et al*., 2018), and such removal and transport of large bedrock blocks has been described by Knight and Burningham (2011) on the Falchorrib-Trawenagh shoreline. Increased wave erosion around the position of HAT on flat shore platforms can result in higher Equotip values when compared to other positions higher or lower in the tidal frame (Knight and Burningham, 2019). The absence of significant variations in Equotip values observed in this study (Figures 2B, 3B) likely reflects a more uniform spread of wave energy across this rectilinear sloping rock shoreline, but may also capture the role of runoff from the hinterland over the higher platform elevations. Some lower Equotip values recorded at and below MHWS may reflect bioweathering of the rock surface, in particular by the barnacle *C. montagui* which occupies this environmental niche (Crisp *et al*., 1981). In summary, although position in the tidal frame can be considered as a first-order control on both rock surface hardness and ecosystems when based on prevailing views in the literature, field evidence shows this is not correct. Surface hardness values vary little with elevation, and cross-correlation between species abundance values shows more complex relationships between different species and shoreline properties. This highlights the interconnections between external and intrinsic factors in influencing rocky shore ecosystems.

CONCLUSIONS

Analysis of rocky shore ecosystems and rock surface properties from an exposed Atlantic-facing shoreline in northwest Ireland reveals complex interrelationships between these components. Species assemblages reflect internal ecosystem dynamics as well as interactions with the rock substrate. The role of surface organisms in variously bioweathering and bioprotecting the substrate impacts in turn on rock surface properties. The Equotip values measured in this study are remarkably uniform irrespective of tidal frame position, suggesting that wave erosion, and possibly runoff, are important in removing any surface weathered material, producing hard, uniform substrates. There is also evidence for bioweathering by intertidal crustacea and mollusca below MHWS, resulting in lower surface hardness values. These relationships highlight the complexity of ecology-substrate patterns. Further, this evidence also suggests that biogeomorphic interactions on rocky shorelines may be more widespread and complex than previously thought.

LITERATURE CITED

Blight, A.J.; Allcock, A.L.; Maggs, C.A., and Johnson, M.P., 2009. Intertidal molluscan and algal species richness around the UK coast. *Marine Ecology Progress Series*, 396, 235-243.

Burningham H., 2008. Contrasting geomorphic response to structural control: The Loughros estuaries, northwest Ireland. *Geomorphology*, 97, 300-320.

Burrows, M.T.; Moore, J.J., and James, B., 2002. Spatial synchrony of population changes in rocky shore communities in Shetland. *Marine Ecology Progress Series*, 240, 39-48.

Chappuis, E.; Terradas, M.; Cafalì, M.E.; Mariani, S., and Ballesteros, E., 2014. Vertical zonation is the main distribution pattern of littoral assemblages on rocky shores at a regional scale. *Estuarine, Coastal and Shelf Science*, 147, 113-122.

Coombes, M.A.; Naylor, L.A.; Viles, H.A., and Thompson, R.C., 2013. Bioprotection and disturbance: Seaweed, microclimatic stability and conditions for mechanical weathering in the intertidal zone. *Geomorphology*, 202, 4-14.

Cooper, J.A.G., 2006. Geomorphology of Irish estuaries: Inherited and dynamic controls. *Journal of Coastal Research*, SI39, 176-180.

Crisp, D.J.; Southward, A.J., and Southward, E.C., 1981. On the distribution of the intertidal barnacles *Chthamalus stellatus*, *Chthamalus montagui* and *Euraphia depressa*. *Journal of the Marine Biological Association of the United Kingdom*, 61, 359-380.

Cullen, N.D. and Bourke, M.C., 2018. Clast abrasion of a rock shore platform on the Atlantic coast of Ireland. *Earth Surface Processes and Landforms*, 43, 2627-2641.

Davenport, J. and Davenport, J.L., 2005. Effects of shore height, wave exposure and geographical distance on thermal niche width of intertidal fauna. *Marine Ecology Progress Series*, 292, 41-50.

Fenberg, P.B. and Rivadeneira, M.M., 2019. On the importance of habitat continuity for delimiting biogeographic regions and shaping richness gradients. *Ecology Letters*, 22, 664-673.

Firth, L.B. and Crowe, T.P., 2008. Large-scale coexistence and small-scale segregation of key species on rocky shores. *Hydrobiologia*, 614, 233-241.

Firth, L.B. and Crowe, T.P., 2010. Competition and habitat suitability: small-scale segregation underpins large-scale coexistence of key species on temperate rocky shores. *Oecologia*, 162, 163-174.

Harley, C.D.G. and Helmuth, B.S.T., 2003. Local- and regional-scale effects of wave exposure, thermal stress, and absolute versus effective shore level on patterns of intertidal zonation. *Limnology and Oceanography*, 48, 1498-1508.

Healy, B., 1996. The distribution of Oligochaeta on an exposed rocky shore in southeast Ireland. *Hydrobiologia*, 334, 51-62.

Jackson, A.C. and McIlvenny, J., 2011. Coastal squeeze on rocky shores in northern Scotland and some possible ecological impacts. *Journal of Experimental Marine Biology and Ecology,* 400, 314-321.

Knight, J. and Burningham, H., 2011. Boulder dynamics on an Atlantic-facing coastline, northwest Ireland. *Marine Geology*, 283, 56-65.

Knight, J. and Burningham, H., 2014. A paraglacial coastal gravel structure: Connell's Bank, NW Ireland. *Journal of Coastal Research*, SI70, 121-126.

Knight, J. and Burningham, H., 2015. The geomorphology of Gola, north-west Ireland. *Irish Journal of Earth Science*, 33, 55-70.

Knight, J. and Burningham, H., 2019. Bedrock hardness values and morphological zonation of a shore platform in South Africa. *Transactions of the Royal Society of South Africa*, DOI:10.1080/0035919X.2019.1670751.

Knight, J. and Harrison, S., 2018. Paraglacial evolution of the Irish landscape. *Irish Geography*, 51, 171-186.

Konar, B.; Iken, K., and Edwards, M., 2009. Depth-stratified community zonation patterns on Gulf of Alaska rocky shores. *Marine Ecology*, 30, 63-73.

Lindegarth, M. and Gamfeldt, L., 2005. Comparing categorical and continuous ecological analyses: effects of "wave exposure" on rocky shores. *Ecology*, 86, 1346-1357.

Long, C.B. and McConnell, B.J., 1999. *Geology of South Donegal: a geological description to accompany the bedrock geology 1:100,000 scale map series, sheet 3 and part of sheet 4, south Donegal*. Dublin: Geological Survey of Ireland, 116pp.

Martins, G.M.; Thompson, R.C.; Hawkins, S.J.; Neto, A.I., and Jenkins, S.R., 2008. Rocky intertidal community structure in oceanic islands: scales of spatial variability. *Marine Ecology Progress Series*, 356, 15-24.

Matsumoto, H.; Dickson, M.E., and Kench, P.S., 2018. Modelling the relative dominance of wave erosion and weathering processes in shore platform development in micro- to mega-tidal settings. *Earth Surface Processes and Landforms*, 43, 2642-2653.

Munroe, D.M. and Noda, T., 2009. Spatial pattern of rocky intertidal barnacle recruitment: comparison over multiple tidal levels and years. *Journal of the Marine Biological Association of the United Kingdom*, 89, 345-353.

O'Connor, N.E., 2010. Shore exposure affects mussel population structure and mediates the effect of epibiotic algae on mussel survival in SW Ireland. *Estuarine, Coastal and Shelf Science*, 87, 83-91.

Ramos, E.; Díaz de Terán, J.R.; Puente, A., and Juanes, J.A., 2016. The role of geomorphology in the distribution of intertidal rocky macroalgae in the NE Atlantic region. *Estuarine, Coastal and Shelf Science*, 179, 90-98.

Sheard, J.W., 1968. The Zonation of Lichens on Three Rocky Shores of Inishowen, Co. Donegal. *Proceedings of the Royal Irish Academy, Section B: Biological, Geological, and Chemical*, 66, 101-112.

Silliman, B.R.; Bertness, M.D.; Altieri, A.H.; Griffin, J.N.; Bazterrica, M.C.; Hidalgo, F.J.; Crain, C.M., and Reyna, M.V., 2011. Whole-Community Facilitation Regulates Biodiversity on Patagonian Rocky Shores. *PLoS ONE*, 6, e24502.

Smith, M.W.; Carrivick, J.L., and Quincey, D.J., 2016. Structure from motion photogrammetry in physical geography. *Progress in Physical Geography: Earth and Environment*, 40, 247-275.

Sorte, C.J.B.; Bernatchez, G.; Mislan, K.A.S.; Pandori, L.L.M.; Silbiger, N.J., and Wallingford, P.D., 2019. Thermal tolerance limits as indicators of current and future intertidal zonation patterns in a diverse mussel guild. *Marine Biology*, 166, 6, doi:10.1007/s00227-018-3452-6.

Stafford, R.; Ng, T.P.T.; Williams, G.A., and Davies, M.S., 2015. A biologically relevant rapid quantification of physical and biological stress profiles on rocky shores. *Ecological Informatics*, 25, 43-48.

Thébaudeau, B.; Trenhaile, A.S., and Edwards, R.J., 2013. Modelling the development of rocky shoreline profiles along the northern coast of Ireland. *Geomorphology*, 203, 66-78.

Underwood, A.J. and Chapman, M.G., 1998. Spatial analyses of intertidal assemblages on sheltered rocky shores. Australian *Journal of Ecology*, 23, 138-157.

Viles, H.; Goudie, A.; Grab, S., and Lalley, J., 2011. The use of the Schmidt Hammer and Equotip for rock hardness assessment in geomorphology and heritage science: a comparative analysis. *Earth Surface Processes and Landforms*, 36, 320-333.

Wilding, T.A.; Palmer, E.J.L., and Polunin, N.V.C., 2010. Comparison of three methods for quantifying topographic complexity on rocky shores. *Marine Environmental Research*, 69, 143-151.