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S Hamylton
University of Cambridge, shamylto@uow.edu.au

Tom Spencer
University of Cambridge, ts111@cam.ac.uk

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Abstract

The idea of landscapes as shifting patch mosaics, structured by a range of biological and physical stochastic forces, is well suited to shallow tropical environments, where seagrass patches lie within a matrix of soft sediments or rocky substrates. The interaction of wave fields and tidal currents with carbonate sediment transport can result in linear morphologies of reef flat material with alternating sand tongues and seagrass beds. Patch-level metrics capture phenomena such as linearity in one variable, which can be evaluated over a gradient of predictable environmental change. Interrogating the statistical properties of patch ensembles enables the links between observed structures and the processes that govern them to be empirically investigated. This study demonstrates how habitat maps derived from remotely sensed Compact Airborne Spectrographic Imager (CASI) data can be used to investigate critical controls of landscape mosaics through the application of geostatistical techniques to Alphonse Atoll, Seychelles.

Keywords

marine, function, structure, linking, landscapes, seychelles, investigation, atoll, alphonse, patterns, seagrass

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An investigation of seagrass patterns at Alphonse Atoll, Seychelles: Linking structure to function in marine landscapes

S. Hamylton[1] and T. Spencer[1]

1) Cambridge Coastal Research Unit, Department of Geography, University of Cambridge, Downing Place, Cambridge, CB2 3EN, UK

ABSTRACT: The idea of landscapes as shifting patch mosaics, structured by a range of biological and physical stochastic forces, is well suited to shallow tropical environments, where seagrass patches lie within a matrix of soft sediments or rocky substrates. The interaction of wave fields and tidal currents with carbonate sediment transport can result in linear morphologies of reef flat material with alternating sand tongues and seagrass beds. Patch-level metrics capture phenomena such as linearity in one variable, which can be evaluated over a gradient of predictable environmental change. Interrogating the statistical properties of patch ensembles enables the links between observed structures and the processes that govern them to be empirically investigated. This study demonstrates how habitat maps derived from remotely sensed Compact Airborne Spectrographic Imager (CASI) data can be used to investigate critical controls of landscape mosaics through the application of geostatistical techniques to Alphonse Atoll, Seychelles.

Key words: Landscape ecology, patch linearity, remote sensing

Landscape ecology is characterised by the empirical investigation of the structure and function of land surface features (Forman and Godron 1986), with particular regard to spatial heterogeneity on biotic and abiotic processes (Risser et al. 1984). The broad scale of a landscape implies that internal processes can be observed across a spectrum of spatial scales, by dividing landscapes into patches, providing a tool for the representation of reality that can be readily understood. Patch-level metrics capture a feature of interest in one variable, which can then be evaluated over a gradient of predictable environmental change. In this way, ecologists are able to quantify and empirically link structure and function at the landscape scale.

Four key requirements for seagrasses are a marine environment, adequate rooting substrate, sufficient immersion in seawater and illumination to maintain growth (Hemminga and Duarte 2000). Seagrass landscapes are composed of seagrasses (marine angiosperms) and unvegetated sediments. Studies of seagrass dynamics at the landscape scale have generally focused on mapping historical change in distribution and cover over time, doing little to link observed structures to underlying processes driving change. Across a gradient of increasing hydrodynamic activity, seagrass beds form patterns that range from continuous meadows to widely dispersed, discrete patches (Fonseca and Bell 1998).

Terrestrial landscape ecologists have developed paradigms on island biogeography and fragmentation that have not crossed over to marine landscapes, which have traditionally focused on patch dynamics (Fonseca and Bell 2006). Sub-littoral landscapes are often viewed as a shifting biological mosaic of multistate systems structured by competition, grazing and predation. Such a viewpoint argues for a shift in focus, from the individual patch to the statistical properties of the entire ensemble. Landscape ecology techniques have emerged as a useful means of investigating functional drivers, such as the influence of wave exposure on community composition (Turner et al. 1999) and the relative influence of internal and external drivers (Fonseca et al. 2008).

Location

Alphonse Atoll (Figure 1) lies at the southern end of the Amirante ridge on the southwestern margin of the Seychelles Plateau, western Indian Ocean. The atoll covers an area of approximately 6x4km and consists of a narrow fore-reef shelf, wide peripheral reef flats and a dish-like lagoon reaching depths of 10m (Spencer et al. 2000). Alphonse is subject to a semi-diurnal tidal regime of range ~2m, upon which reversing monsoons control the direction and strength

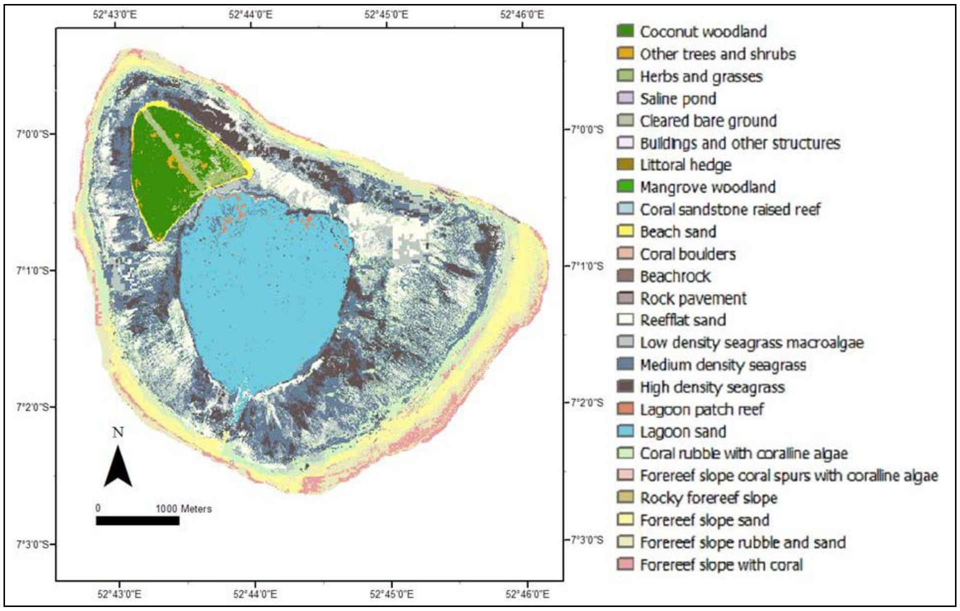

Figure 1. A habitat map of Alphonse Atoll, Southern Seychelles, West Indian Ocean (7^{o}S, 52^{o}E).

of surface currents. However, for the majority of the year, Southeast Trade winds dominate incident wave activity. The upper fore-reef exhibits distinct coral spur and groove formations. These extend around the atoll perimeter, being particularly well developed on the south-east and north-western windward coastlines. A distinctive feature of the adjacent reef flat is alternating linear tongues of seagrass on carbonate sediments. Similar features can be observed on many Indian Ocean reef flats and the aim of this paper is to investigate the functional role of spur and groove morphology, along with wave power, as drivers of these linear seagrass structures on the reef flat

Methods

A habitat map was generated from remotely sensed data acquired with an aircraft-mounted Compact Airborne Spectrographic Imager (CASI). Seventeen spectral bands of data were acquired at a spatial resolution of 1 sq.m, yielding synoptic coverage of the area of interest. Following geocorrection, flight strips were mosaiced using a band-wise linear colour balancing model to minimise across-track variance, with histogram matching to adjust for radiance offsets. Image bands were corrected for the effects of light absorption and scattering in the water by approximating the vertical radiative transfer through a water column to a logarithmic decrease with increasing depth (Lyzenga 1981). Training areas derived radiance measures over a number of spectral subclasses to build up statistical populations of habitat classes apparent in the image feature space. A maximum likelihood classification was performed on depth invariant bands, assigning each pixel of the image to the most likely habitat class on the basis of statistical probability. Map accuracy was assessed by exporting 283 polygon centroid coordinates to a hand-held GPS and comparing the corresponding location in the field to the habitat type recorded on the map. Overall accuracy was defined as the total number of correct patches divided by the total number of patches in the validation assessment.

Field data were collected on spur and groove depths and wave power was empirically modelled to derive information on potential drivers of seagrass patch structure as a response variable. Gustafson and Parker (1992) developed a metric for assessing patch linearity based on the premise that elongated patches of a given area are comprised of pixels closer to their edges than square patches of the same area:

$$\text{LINEAR} = \frac{\left[\frac{a_{ij}^{*}}{(2b-r)^{2}}\right] - 1}{a_{ij}^{*}} \qquad \textit{Equation 1.}$$

where a_{ij}^{*} =area of patch ij in terms of number of cells, and b = average cell value of the pixels comprising the patch. r = 0 if the patch contains side by-side pixel rows; 1 if not.

Six analysis windows were established in the centre of the reef flat to investigate seagrass community structure around the atoll. Linearity was calculated step-wise for each patch by calculating Euclidean distance from patch boundaries and averaging pixel values across patch spatial extents. A focal rank operator was used to record the number of pixels in the immediate neighbourhood with a value less than the centre pixel. For each pixel of the input distance surface local maxima were returned as zero values in an output thematic layer. An optimal sample window size was defined using an experimental semivariogram. This was calculated by sequentially comparing the linearity of each individual patch to the rest of the patches in the map via the Moran statistic and plotting these values against the distance between patches. The lag distance at which the maximum semivariance was reached for linearity of all seagrass patches within the landscape was found to be 300m; hence this was adopted as the sample window dimensions.

Field measurements of groove depths were made using a Norcross DF2200PX handheld bathymetric sounder. A 50m transect was established along a defined bearing, along which a diver swam at a constant depth above the spur and groove morphology, perpendicular to the direction of groove alignment. GPS locations were recorded at both ends of the transect and depth measurements were recorded at 1m intervals.

Wave power was calculated using an amended version of the approach described by Roberts (1974). Transects of 5km length were established across the atoll cross section, running towards the lagoon centre, at ten degree intervals around the atoll. A bathymetric map facilitated derivation of a shoaling coefficient for each pixel for a given depth to wavelength ratio. Additionally, a refraction coefficient was calculated from the change in angles between the waves and shoreline and wave velocity (Weigel 1964). Mean wave height and period were hindcast for the outer point of each transect using data on wind strength, frequency and fetch taken from the Indian Ocean volume of the *Marine Climatic Atlas of the World* (US Navy 1958). Wave height was then computed for each pixel along the transect as a function of the wave height at the previous interval, change in shoaling coefficient, and change in refraction coefficient.

The influence of water movement was investigated on seagrass structure by carrying out regressions of patch linearity against independent variables at two spatial scales. In the first instance, descriptive bivariate regressions were used to explore the separate influence of "groove depth" and "wave power" on the linearity of patch assemblages within analysis windows. Geographical variation in the residuals of these bivariate models was reviewed to investigate additional model covariates. Multivariate regression was used inferentially to extend statements about the mean patch statistics from sample windows to the patches comprising the rest of the atoll habitat map. Tests were run to ensure the assumptions of multiple regression were met.

Results

Figure 2 summarises the geographical distribution of the information collected. Key points to note include:

-A good quality image classification was achieved, providing a clear and accurate representation of the heterogeneity apparent in the raw image (overall accuracy = 77%)

-Upper terrace spur and groove adjacent to the survey windows was well pronounced on the southeast and northwest faces of the atoll, where deep grooves were prevalent (Fig. 2).

-Lower relief spur and groove was recorded adjacent to the remaining sites, where wider, less frequent spurs divided shallower grooves.

-The wave power model indicated that the southeast-facing coastline of the atoll was subject to higher energy levels than the remainder of the atoll

-Computed values for the linearity metric (Equation 1) ranged between 0.22 and 0.67 for seagrass patches on the reef flat.

Bivariate regressions of groove depth and wave power with linearity values for seagrass patches falling inside adjacent survey sites on the reef flat revealed moderate positive correlations (Table 1). This suggested that the better "developed" the spur and groove morphology, the more linear the adjacent seagrass patches.

Descriptive bivariate regressions: Functional characteristic Vs Linearity	**R^2**
Average groove depth v Linearity	0.581
Average wave power v Linearity	0. 431
Multicolinearity check	
Average groove depth v Average wave power	0.397
Inferential multivariate regression	
Groove depth and wave power v linearity	0.813

Table 1. Diagnostics for the descriptive bivariate and inferential multivariate regressions of seagrass linearity against groove depth and wave power, individually and collectively.

The groove depth and linearity bilinear regression gave rise to positive residuals on the west side of the atoll and negative residuals on the east side, approaching unity in the southeast. Comparison of the groove depth and wave power model revealed both variables to be at a maximum on the southeast region of the atoll. The east side is subject to high energy levels relative to shallow groove depth, whereas the west side has deeper grooves and lower energy in relative terms. The combined influence of adjacent groove depths and incident wave power explained 81% of the variation in seagrass patch linearity across the overall habitat map.

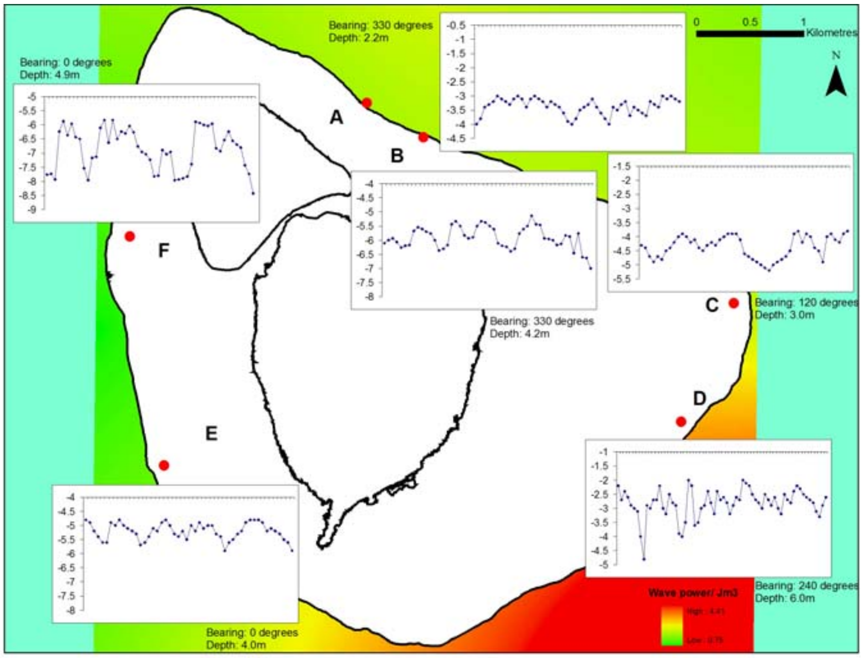

Figure 2. Analysis sites at Alphonse. Profiles of adjacent spur and groove, superimposed onto the wave power model. Each spur and groove profile represents a 50m transect across the given depth and bearing. Incident wave power ranges from 4.41-0.75Watts per cubic metre.

The estimated regression function reads:

$$\text{Patch linearity} = -0.234 + 2.584\text{x}10^{-3*}\text{wind factor} + 3.93\text{x}10^{-3*}\text{groove depth}$$

T-test values were 9.337 and 12.429 for the mean wind force and groove depth respectively (561 degrees of freedom; $p<0.001$), suggesting it to be highly likely that the estimated coefficients are different from zero. Diagnostics indicated compliance with the assumptions of multiple regression.

Discussion

In general, seagrass patches on the reef flat are more linear than the overall habitat mosaic at Alphonse (0.2). Linear morphologies are likely a patch scale response to the hydrodynamic setting on the reef flat; such bed forms have been observed for *Posidonia australis* (Cambridge 1975), *Cymodocea nodosa* (Marbà and Duarte 1994) and *Zostera marina* (Fonseca and Bell 1998). Alternate dark and white stripes were also noted on aerial photographs of Mayotte Barrier Reef (Guilcher et al. 1965). This is in accordance with descriptions of shallow seagrass beds on Indian Ocean reef flats as "stripey zigzag" patterns (Den Hartog 1971).

Given these linkages, the spatial pattern of linearity among seagrass patches can be linked to the absolute amount of energy reaching the coastline as a result of wind-driven surface waves, as confirmed by the bivariate regression ($R^2=0.43$). The plan-view pattern is one of abundant alternating linear patches of seagrass and sand in the Southeast and Northwest of the atoll, with lower values in the Northeast. The amount of energy reaching a shore is influenced by water depth, which is controlled by wave-setup and tides. Setup, the rise in mean water level above the still-water elevation of the sea due to waves breaking, is a significant determinant of reef-top sediment transport (Komar 1976). Experimental results have found wave setup and flow to increase with increasing off-reef wave height and period, and with decreasing reef top water depth (Gourlay 1996). Tides operate at a lower frequency and determine the geomorphic work that can be carried out on reef flats in two ways: through unidirectional currents with a diurnal tide frequency and by tides modulating reef flat wave energy through water level. At low tide, waves break on the reef edge and no significant energy is propagated across the reef top. However, at high tides, depth-limited waves are able to propagate across the reef-top. Such a distinction is important at Alphonse, where the ~2m tidal range coincides with the height of the reef crest.

Collectively, setup and tides separate out the influence of *(i)* wind-driven surface waves, and *(ii)* subsurface currents. This separation, along with the absence of multicolinearity between the explanatory variables of wave power and groove depth, justifies the inclusion of two functional drivers operating at different depths of the water column. The geographical distribution of residuals from the groove depth vs. linearity bilinear regression revealed spatial structure that suggested additional independent variables to have been omitted from the model would have elevated values relative to groove depth on the east side of the atoll and lower relative values in the west, as was the case with wave power. The multivariate regression encompassed processes that differed in the nature of their influence on the independent variable, as evidenced by the greater level of explanatory power of the multivariate model.

The comparison of the distribution of patch linearity to adjacent spur and groove morphology may be explained by the transformation of energy from the outer to inner sections of the reef complex. Spurs contribute to energy dissipation through the action of bottom friction against subsurface currents on the upper terrace. Frictional attenuation over spurs lowers the energy available for particle entrainment, inducing deposition closer to the reef crest. In areas adjacent to grooves, lower lying topography and a smaller surface may promote extended entrainment, producing sand tongues that extend further onto the reef flat. An energy attenuation profile could therefore be established for landward-moving reef flat water that reflects the spur and groove topography further offshore.

Conclusion

Overall, it was found that spur and groove morphology (as measured by groove depth) and incident wave power had a moderate influence on reef flat seagrass patch linearity when treated independently, with greater explanatory power in a combined model.

The distinction between the two regression steps taken in this study highlights the importance of technique in landscape ecology studies. The bivariate regressions were "descriptive", in that they were carried out on patch assemblages inside analysis windows chosen to describe the apparent seagrass patterns as a representation of variation in a response variable where all covariates were not necessarily present in the model. Geographical variation in the residuals from this step was a useful basis for addition of a covariate that enhanced the explanatory power of the model and allowed the descriptive statement to be extended to the whole habitat map.

The transition from descriptive to inferential modelling highlights the importance of good representation of both structural and functional phenomena that are commonly the focus of landscape ecologists. This analysis of patches (as the fundamental unit of habitat maps produced from remote sensing data), using landscape ecology techniques demonstrates the suitability of these combined tools for the specification, development and testing of empirical models that link structure and function in marine landscapes.

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