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Spatial modelling of benthic cover using remote sensing data in the Aldabra lagoon, western Indian Ocean

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Spatially explicit ecological modelling was used to predict the distribution of 4 benthic components (live coral, carbonate sand, macroalgae and dead coral) inside the Aldabra lagoon, southern Seychelles, western Indian Ocean. Both classic ordinary least-squares and spatial autoregression techniques were carried out on a field data set of 774 spatially referenced records and 3 satellite remote sensing images to define an empirical relationship between local environmental conditions (water depth and water level variation) and benthic cover. This relationship was then used to generate a synoptic model of the spatial cover and distribution of each benthic component at the landscape (i.e. whole lagoon) scale. Environmental conditions were estimated from satellite remote sensing data (water depth) and using GIS techniques (water level variation). By drawing on species–environment relationships applicable to many lagoons, continuous records of percentage benthic cover were derived for the extensive lagoon (174 km2) at a high measurement level (ratio) for use in conservation and resource management applications. The transition from the ordinary least-squares model to the spatially lagged model was accompanied by a marked growth in predictive power (R2 = 0.25 to 0.79), indicating that neighbourhood context interactions play an important role in determining benthic cover of the Aldabra lagoon.

Keywords

lagoon, sensing, spatial, modelling, western, indian, ocean, data, benthic, cover, aldabra, remote, GeoQUEST

Disciplines

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Spatial modelling of benthic cover using remote sensing data in the Aldabra lagoon, western Indian Ocean

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Abstract

The present study uses spatially explicit ecological modelling to predict the distribution of four benthic components (live coral, carbonate sand, macroalgae and dead coral) inside the Aldabra lagoon, southern Seychelles. Both classic ordinary least squares and spatial autoregression techniques are carried out on a field dataset of 774 spatially referenced records and three satellite remote sensing images to define an empirical relationship between local environmental conditions (water depth and water level variation) and benthic cover. This relationship is then used to generate a synoptic model of the spatial distribution and configuration of each benthic component at the landscape (i.e. whole lagoon) scale. Environmental conditions are estimated from satellite remote sensing data (water depth) and using GIS techniques (water level variation). By drawing on species-environment relationships applicable to many lagoons, continuous records of percentage benthic cover are derived for the extensive lagoon (174 km^2) at a high measurement level (ratio) for use in conservation and resource management applications. The transition from the ordinary least squares model to the spatially lagged model is accompanied by a marked growth in predictive power (R^2 = 0.25 to R^2 = 0.79), indicating that neighbourhood context interactions play an important role in determining benthic cover of the Aldabra lagoon.

Spatial regression, coral reef, Seychelles, atoll, autoregression, autocorrelation

1 Introduction

The lagoons of coral atolls promote marine primary productivity by enhancing the residence time of oceanic waters (Charpy and Ruboud-Charpy, 1990; Delesalle and Sournia, 1992) and provide calm, stable environments within depth ranges that are commonly able to support

highly diverse benthic communities including mangroves, corals, seagrasses and macroalgae that provide refugia for coral reef fishes (Leis 1994; Dufour and Harmelin-Vivien, 1997). An understanding of the benthic composition of atoll lagoon floors and the environmental factors influencing the ecological goods and services they provide is therefore needed to inform conservation practice, particularly the spatial planning of marine reserves (Roberts et al., 2003; Sobel and Dahlgren, 2004; Almany et al., 2009).One of the key challenges to the characterisation of atoll lagoon benthic composition is the paucity of datasets available in these frequently large but remote environments. Typically, lagoon datasets at the landscape scale are characterised by a widespread coverage of abiotic data (e.g. remotely sensed reflectance or bathymetric swath datasets and their derivatives), but only point samples of benthic communities (e.g. phototransects and associated detailed community inventories) (Lehmann et al. 2003; Schumchenia and King, 2010; MacClanahan and Karnauskas 2011).

Spatially explicit ecological modelling approaches can be used to extrapolate locally sampled records to synoptic landscape-scale (10 – 100 sq.km) information on biological coverage distribution using techniques such as generalized linear regression, generalized additive models, ordinary least squares regression and boosted regression trees (see Table 1 for a summary of recent studies). Two key advantages with these approaches are that they do not require extensive landscape-scale ecological field surveys, which can be costly and a logistical challenge to achieve, and that they draw on species–environment relationships to develop benthic cover models in an ecologically meaningful manner. A recent assessment of the effectiveness of surrogates for marine biological diversity used in 264 published studies found that in many instances they provide a robust indication of marine benthic community properties. The primary reason for aspects of their poor performance was the differing rates of spatial variation in biological diversity and the surrogates invoked, a phenomenon that effected tropical reefs above temperate reefs and soft bottom habitats due to their high

biological complexity, which is strongly correlated to environmental diversity (Mellin et al. 2011).

Environmental controls on coral reef benthic community character include water depth and associated light availability, hydrodynamics, the presence of suspended and settled sediments, water temperature and nutrient availability (Done, 2011). These biophysical variables are themselves geographically structured, resulting in distinctive ecological and geomorphological zonation patterns that transcend the reef systems of the Atlantic, Caribbean and Indo-Pacific regions (Blanchon, 2011). This geographical structure commonly gives rise to spatial autocorrelation whereby spatially structured processes and neighbourhood interactions underpin correlation among multiple records of a single reef benthic community character that itself is strictly attributable to their relative locational positions. From a statistical standpoint, spatially explicit techniques have several advantageous features that make them particularly useful for the development of ecological models of benthic community character. These include *i.* the ability to quantify the extent and patterning of autocorrelation across reefs, *ii.* the ability to index the nature and degree to which a fundamental assumption of classic, (non spatial) statistical techniques is violated, e.g. the independence of observations, *iii.* the ability to indicate the nature (endogenous vs. exogenous) of an observable spatial pattern, and *iv.* the ability to utilise components of neighbouring ecological communities as a surrogate for a missing variable. These advantages have been well recognised and incorporated into terrestrial community ecology studies (Lichstein et al. 2002; Beale et al. 2007; Dray et al., 2012). Despite these advances, spatial autocorrelation is seldom incorporated into ecological modelling studies on coral reef systems, representing a significant methodological gap that has the potential to benefit coral reef studies. For example, the one study listed in Table 1 that did incorporate spatial autocorrelation into the modelling procedure found that this doubled the power of the model for explaining species abundance (Mellin et al., 2010).

The present study draws on the advantageous characteristics of spatially-explicit approaches by invoking a method that accounts for spatial autocorrelation of lagoon benthic communities which often derives from the geographical structure of marine ecological processes such as disease, competition and community recruitment dynamics (Stevens, 2005). Two different regression models are used to predict the spatial distribution of benthic cover types (live coral, carbonate sand, macroalgae and dead coral) inside the large Aldabra lagoon, using the environmental parameters of water depth and water level variation. These parameters play a large role in determining the physical environmental drivers of water renewal time (Andrefouet et al., 2001), hydrological regime (Pages and Andrefouet, 2001), wave stress, tidal currents (Kraines et al., 2001), water exchange and wave pumping (Adjeroud et al. 2000) and bathymetry (Leclerc et al., 1999) which are all known to important determinants of the distribution of biological communities in coral reef lagoons. Furthermore, these environmental parameters can be readily derived and robustly characterised from remotely sensed imagery, often with a root mean square error <0.3m (Stumpf et al., 2003). The first model uses ordinary least squares regression, while the second model introduces a spatially lagged term to account for autocorrelation in the environmental parameters. As far as we are aware, this is the first application of spatially lagged autoregressive modelling to the distribution of atoll lagoon benthos.

Aldabra Atoll is a particularly appropriate site at which to undertake such a modelling exercise. The lagoon covers an area of 174 km^2, making it one of the largest enclosed atoll lagoons in the Indian Ocean (Andréfouët et al., 2009). This large size allows for the development of spatial gradients in environmental controls; water depths in the lagoon vary from over 20 m in the main channels to < 5m in the central lagoon and the atoll's east - west orientation under a SE Trade wind regime for much of the year produces clear variations in

wave climate regime within the lagoon. Information from this location is also of regional significance since Aldabra Atoll was designated a UNESCO World Heritage Site in 1982 because of its isolated position and largely unexploited natural resources, which have preserved a wealth of both terrestrial and shallow marine biodiversity (Stoddart, 1968; Hillary et al., 2002). The Aldabra lagoon therefore provides not only an anthropogenically undisturbed system in which to define biodiversity – environment relations, but also a benchmark of lagoon benthic biodiversity in a region heavily exploited and impacted by human pressures (northern Madagascar, Comores and East Africa).

Spatially explicit ecological modelling studies on coral reef and associated communities	**Reference**
Generalized regression analysis and spatial prediction models link a coral reef fish diversity index to depth, fish and habitat characteristics	Garza-Perez *et al.* 2004
Generalised additive models link reef bottom features (topographic complexity, sand-sediment, rock-calcareous pavement, rubble) to water depth and light reflectance	Arias-Gonzales *et al.*, 2011
Linear regressions and canonical correspondence analysis link ecological variables (parrotfish, surgeonfish, and total herbivore abundance, numbers of fish species and the percent cover of functional groups) to physical attributes, including distance of site to the nearest channel, current mean and variability, and current maximum	MacClanahan and Karnauskas 2011
Cellular automaton models simulate coral community dynamics in relation to recruitment and disturbance	Langmead and Sheppard, 2004
Linear regression links the beta diversity of coral reef communities to water depth and wave exposure	Harborne *et al.* 2006
Boosted Regression Trees (BRT) and Maximum Entropy Species Distribution Modelling predict coral reef fish distribution on the basis of topographic complexity and geographic location across a reef platform shelf	Pittman and Brown, 2011
A Bayesian meta-analysis of the effectiveness of biological surrogates for predicting marine biodiversity	Mellin et al. 2011
Monte Carlo Simulations and linear regression link benthic rugosity and evenness to the abundance of reef fishes	Purkis et al. 2008
Boosted regression trees link LiDAR derived topographic complexity to the diversity and abundance of fish and corals	Pittman et al. 2009
Generalized Linear Models predicted juvenile fish species richness and abundance across a range of spatial scales from remotely sensed habitat maps	Mellin et al. 2007
Generalized linear mixed-effects models (GLMMs) predicted species richness and abundance of coral reef fishes from environmental variables including depth, sea surface temperature, salinity and nutrient concentrations	Mellin et al 2010

Table 1 Spatially explicit ecological modelling studies on coral reefs and their associated communities

1.1 Study location

Aldabra Atoll (90 24' S, 460 20' E) lies 420 km northwest of Madagascar and 620 km east of the African continental mainland (Figure 1). The lagoon accounts for almost half the total atoll area of 365 km^2 and is larger than the encircling land area of elevated (average + 4.5 m, maximum 8 m) Pleistocene reef limestones (155 km^2, including the two rocky islands in the lagoon, Ile Esprit in the south west, and Ile Michel in the east) (Stoddart et al., 1971). The lagoon is drained by *i.* two main channels: Grande Passe (between Polymnie and Ile Picard) and Passe Houareau (between Grande Terre and Ile Malabar); *ii.* a small, deep channel, Passe Gionnnet, between the two islands (Polymnie and Ile Malabar) along the north coast; and *iii.* a series of shallow channels, the West Channels, between Ile Picard and Grande Terre (Figure 1). Grande Passe, 300m wide at its entrance, extends 6 km into the lagoon in a bifurcating network of near vertically-sided and flat-floored channels. These channels maintain depths of 20 m for 3km into the lagoon and remain 10 m deep until near their lagoonal limits. Maximum depths of 15 m and 9 m characterise Pass Houreau and Passe Gionnet respectively but only Passe du Bois is deeper than 5 m in the West Channels (Stoddart et al., 1984).

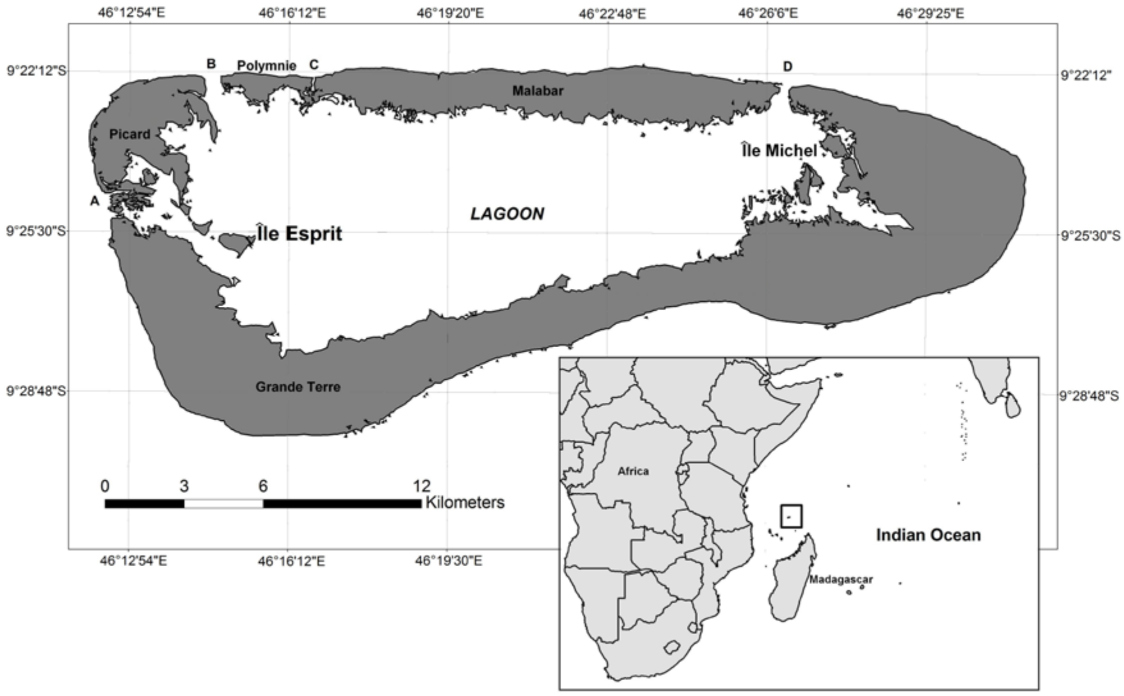

Figure 1. Aldabra Atoll. Inset: The location of Aldabra Atoll in the western Indian Ocean and wind rose depicting frequency with which wind blows from the cardinal and subcardinal directions (days per year). Channels are labelled as follows: A: Western channel network, including Passe du Bois, B: Grande Passe, C: Passe Gionnet, and D: Passe Houareau.

Lagoon shores are either undercut limestones, the degree of intertidal notching varying with exposure (Taylor, 1971), or mangrove-fringed, with mangrove forests (high and low), thickets and fringing belts (Macnae, 1971). Lagoonal cliff recession has left numerous ‘mushroom’ rocks on shore platforms around the lagoon. The lagoon is rock-floored, flat and smooth, quite unlike the karstic topography of many large atoll lagoons (e.g. Shepard, 1970; Purdy, 1974; Menard, 1982) and only thinly veneered (typically 30 cm, maximum thickness of 1 m) with sediments (Stoddart et al., 1971). Farrow (1971) identified three lagoonal sedimentary environments - sandflats, carbonate mudflats and mangrove mudflats - and Taylor (1978) provided an initial map of lagoon sediments, showing that a large area of the lagoon is sediment-free. The mean spring tidal range of 2.74 m at Aldabra is high by oceanic atoll standards but reduces rapidly within the lagoon; thus at Pass Houareau, the oceanic tide of over 3 m is reduced to 1.2 m within 500m of the channel mouth (Farrow and Brander, 1971).

At low neap tides much of the lagoon becomes dry, with the rock basement subject to ponding in local bathymetric depressions (Potts and Whitton, 1980).

2 Material and Methods

2.1 Model dependent variable: Field measurement of benthic cover statistics

The coverages of different benthic classes (live coral, bare carbonate sand, macroalgae and dead coral) were sampled from a stationary boat at 486 ground reference locations distributed throughout the lagoon (Figure 2). Data records consisted of a snapshot (typically 30 seconds), covering an area of 10 m^2 of oblique underwater video footage taken from a Seaviewer drop cam 950 mounted on a submarine cable. At each video referencing point (the depths of which ranged across the lagoon from 1 m to approximately 20 m), the tethered underwater video camera was lowered from the boat and held so that it drifted approximately 10 cm above the lagoon floor. Depth was measured using a HawkEye single beam bathymetric sonar sounder and the geographical position of each footage sample was recorded by a differential GPS on the boat (positional accuracy ± 0.2m). A weight was attached to the base of the videocamera so that it dropped rapidly through the water column to minimise drift error. The rapidity of video camera deployment permitted efficient ground referencing over an extensive area of the lagoon. This would not have been possible using traditional SCUBA diving approaches during the limited (3.5 week) fieldwork period.

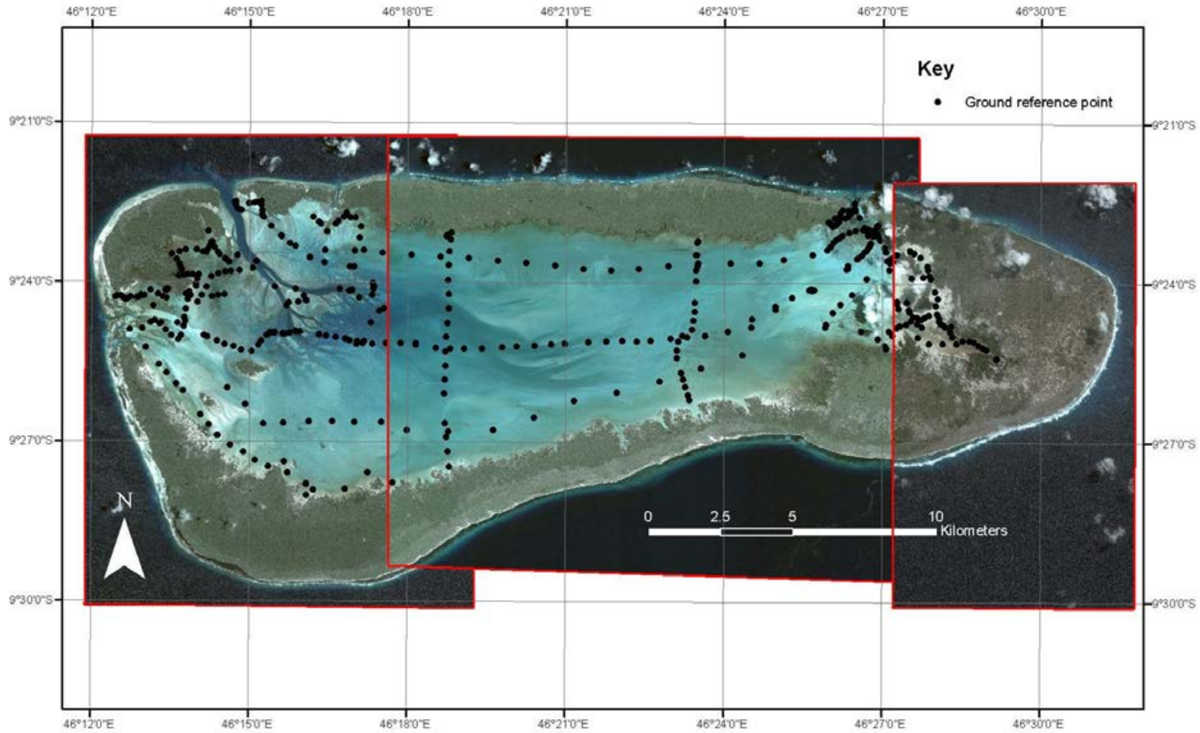

Figure 2. Field sampling at Aldabra Atoll, 16th January – 11th February 2009. Black dots depict ground reference points, red outlines illustrate the extent of each satellite image used. From West to East, the three images were acquired on February 4th, February 6th and March 6th 2001 respectively.

Each thirty second record of sample video footage record was viewed and the proportion of benthic cover (% cover) was visually estimated for the 4 classes: live coral, bare carbonate sand, macroalgae and dead coral. Percentage cover was chosen in order to standardise between different areas covered during the period of video camera operation due to variations in boat speed and water current. In addition to the video snapshots, 287 photographs were taken using a Nikon F90X in a Nexus underwater housing as additional ground referencing points to assess the accuracy of the models generated. These were assessed for substrate type and cover using the computer programme 'Coral Point Count' (Kohler and Gill 2006), in which 20 spatially random points were distributed on each photograph. The feature underlying each of the 20 points was identified and the coverage of each of the 4 benthic classes was estimated for each location (Kohler and Gill, 2006).

2.2 Model independent variables: Water depth and level variation

Three QuickBird satellite images covering the study area with a spatial resolution of 1 m were used to derive the water depth of each image pixel (see Figure 2 for coverage of three images). The images were acquired on February 4th, February 6th and March 6th 2001. As a pre-processing step, each image was atmospherically corrected using empirical line methods (Karpouzli and Malthus, 2003).

2.2.1 Water depth model

A band ratio transformation was applied to the three satellite images to derive the water depth of each image pixel. This method established a relationship between the changing ratio of two atmospherically corrected water penetrating waveband pairs at green (560 nm) and blue (485 nm) wavelengths and water depth (Stumpf et al., 2003). This was done using 15 readings that were taken *in situ* and corrected to a common vertical datum of mean sea level, determined by measuring semi-diurnal tidal cycles with a pressure transducer and Campbell 21X Micrologger in Passe du Bois. Resulting depth estimations were then compared to an additional 188 point water depth measurements recorded in the field, which were corrected to mean sea level.

2.2.2 Water level variation model

Two energy sources were considered for the estimation of water level variation in line with the lagoon circulation models outlined by Wiens (1962): *i.* exposure to wind-driven waves, and *ii.* tidally driven subsurface currents. Due to the substantial tidal range, water circulation patterns are tidally driven with secondary wind influence on the water column surface layer, particularly from the southeast because of the extensive nature of the lagoon (approximately 35 km across its primary axis), (Farrow and Brander, 1971; Schott and McCreary, 2001). A first order model of overall water level variation across the extent of the lagoon, X_2, was calculated as the product of tidal, M_t, and wind-driven, M_w, circulations (Equation 1):

$$X_{21} = M_t \sum_{1}^{8} M_w \qquad \text{Equation 1}$$

Tidally driven flow, M_t, was restricted to the channels linking the lagoon to the open ocean. To derive this term, a simple model of the spatial distribution of flow in relation to these channels was generated on the basis of the distance from each channel opening. Distances further away from channels were less influenced by tidal circulation than those closer to channels, with the influence decreasing in a linear fashion due to friction with distance from channel opening (linear bottom friction coefficient, K, of 0.015 and 0.024ms^{-1} for Passe Houareau and Grande Passe respectively) (Pugh, 1979; Pugh and Rayner, 1981). A spatially explicit application of this distribution model was executed in ArcGIS 10 by creating a point surface that defined the centre point of each channel opening at the outer point of the lagoon rim and generating a raster dataset across the whole lagoon in which pixel values represented the Euclidean distance from the nearest channel opening. For each pixel, the linear model was applied to calculate subsurface water flow with the larger friction coefficient applied to those channels where subsurface features such as coral heads and sand megaripples were apparent and the smaller coefficient applied to Grande Passe, where the bottom was subject to scouring (Farrow and Brander, 1971).

A GIS-based generic model for estimating relative wave exposure (GREMO) was used to estimate the influence of wind waves, M_w, using GIS techniques to estimate incident power on the basis of fetch lengths summed for 8 cardinal and subcardinal directions and local wind field data (Pepper and Puotinen, 2009). To define fetch lengths across the study area, a land boundary outline was created using the infrared band of the three QuickBird images. Areas of high infrared signal were interpreted as land and converted to a vector layer. All land polygons were deleted to produce a data layer in which areas over water had a value of 1 and those over land had a value of 0. A 30 m interval point grid was placed over the study area and the radiating lines extension tool in ArcView10 (Jenness, 2006) was used to generate 8

lines, each 20 km in length, spaced 45 degrees apart, originating from each grid point (Pepper and Puotinen, 2009). All fetch-limited lines (i.e. those intersecting an overlaid coastline shapefile) were trimmed at the point of intersection with the coastline of the inner atoll rim. Polyline lengths were then summed for each gridpoint and input as fetch distances from each direction into the relative wave exposure model. Wind field data were acquired from the WaveWatch III application developed by the National Oceanographic and Atmospheric Administration (for further details see Tolman, 2002). Records of mean monthly wind strength at an elevation of 10 m were exported for the southern Seychelles cell at 7 degrees south and 52 degrees east, weighted to account for frequency from each of the cardinal and subcardinal directions and input into the model to reflect cumulative influence of wind distribution and strength across a 5-year period (2000 – 2005).

2.3 Model Construction

The two regression procedures, ordinary least squares (classic) regression and spatially lagged autoregression, were carried out using the set of 486 data cases in the software GeoDa (Smirnov and Anselin, 2001). Each data case represented a sample location inside the lagoon for which there was a field measure of benthic cover (dependant variable) and associated modelled values for water depth and water level variation (independent variables). The two types of regression analysis were carried out in sequence. Firstly, for the 486 ground reference locations, the coefficients of variation β_0 to β_{02} were determined and the proportion of variation accounted for by each benthic cover model was measured. Secondly, for a spatially continuous grid of 1m interval points across the whole lagoon, a predicted value and residual for each benthic cover type was generated. For the classical regression procedure, cases were input into Equations 2 and 3.

$$Y_{(i)} = \mu_{(i)} + e_{(i)} \qquad i = 1, \ldots, n \qquad \text{Equation 2}$$

$$\mu_{(i)} = \beta_0 + \beta_1 X_{1(i)} + \beta_2 X_{2(i)} \qquad \text{Equation 3}$$

where n = the number of points or areas

X_1 *and* X_2 are the independent variables of water depth and movement respectively

$e(i)$ = independent, normally distributed error term

β_0 and β_2 = coefficients estimated using the model.

In the second regression model, a spatially lagged autoregressive term was introduced as an independent variable. This approach explicitly drew on the location of each individual case through the construction of a spatial weights matrix ($w_{(i,j)}$) that expressed for each case, those locations that belong to its neighbourhood, such that w_{ij}=1 when i and j are neighbours and w_{ij}=0 otherwise (Anselin and Bera, 1998). The values of the dependent variable at neighbouring locations were therefore introduced into Equation 4:

$$\mu_{(i)} = \beta_0 + \beta_1 X_{1(i)} + \beta_2 X_{2(i)} + \rho \sum_{j \in N(i)} w(i,j) Y(j) + e_{(i)} \quad i = 1, \ldots, n \qquad \text{Equation 4}$$

where ρ = a parameter associated with the interaction effect (Haining, 2003).

To estimate the autoregressive terms in the spatial lag model, all cases and the spatial weights matrix were input into a maximum likelihood procedure that generated consistent estimates of ρ and β. A distinguishing feature of the likelihood for linear regression parameters with a spatial autoregressive component is a Jacobian term of the form $|I - \rho W|$, an evaluation of which was carried out based on the characteristic polynomial of the spatial weights matrix, W, to maximise the likelihood function of this term.

After each regression analysis, the output function was used to predict benthic cover continuously across the lagoon, diagnostics were recorded and the spatial distribution of model residuals was mapped. For the classical regression, diagnostics included the Moran's I Statistic for spatial autocorrelation. The Statistic measures the tendency for similar values to be located close together in space. Values close to -1 indicate strong negative autocorrelation (a tendency for dissimilar values to be close together), while values close to 1 indicate strong

positive autocorrelation (a tendency for similar values to be close together), and values close to 0 indicate a lack of association. For the spatial regression, diagnostics consisted of the estimated coefficients and their asymptotic errors, T-test and measures of fit. Finally, by way of validation, the predicted proportions of the 4 benthic cover classes (live coral, bare carbonate sand, macroalgae and dead coral) were compared to the 287 underwater photographs and the correspondence between the two was assessed via a linear regression.

3 Results

3.1 Field measurement of benthic cover

Many of the ground reference points visited supported a mixture of benthic cover components. However, the most prevalent benthic cover class observed in the Aldabra lagoon was macroalgae, which dominated at 64% of the ground reference points (see Table 2 for average coverage values across the 486 ground reference points).

Benthic cover	**# Samples**	**Average depth/ m**	**Dominant benthic cover classes**
Live coral 	67	4	48% live coral 20% dead coral 16% rubble 16% coralline algae
Bare carbonate sand 	76	2	74% sand 10% algae
Macroalgae 	310	1	70% *Hypnea esperi* 20% *Enteromorpha* sp. 10% *Caulerpa* spp.
Dead coral 	33	2	70% rubble 20% dead coral

Table 2. Ground reference points collected for benthic cover components of the Aldabra lagoon; example photographs illustrate benthic covers on the left; coverage statistics have been averaged for all video footage samples within each group and only dominant classes are reported, which do not sum to 100%

3.2 Model independent variables: Water depth and water level variation

The water depth model inside the study area predicted depths, relative to mean sea level, that ranged between a minimum value of 0.2 m above reef patches and a maximum value of 30 m inside Grande Passe in the northwest of the lagoon (Figure 3). These predictions closely approximated the values of 188 validation points measured *in-situ* with a bathymetric sounder and corrected to mean sea level by removal of tidal fluctuations as recorded at Passe du Bois in the Western lagoon throughout the fieldwork period (R^2 = 0.95). The water depth model inside the study area predicted depths that ranged between 0.2 m above reef patches and 20 m inside Grande Passe in the northwest of the lagoon. After correction to a vertical datum of mean sea level with data from the tide gauge, these closely approximated the 188 values measured *in-situ* with a bathymetric sounder and (R^2 = 0.95). The distribution of water level variation was such that it was elevated at either end of the lagoon (Figure 3).

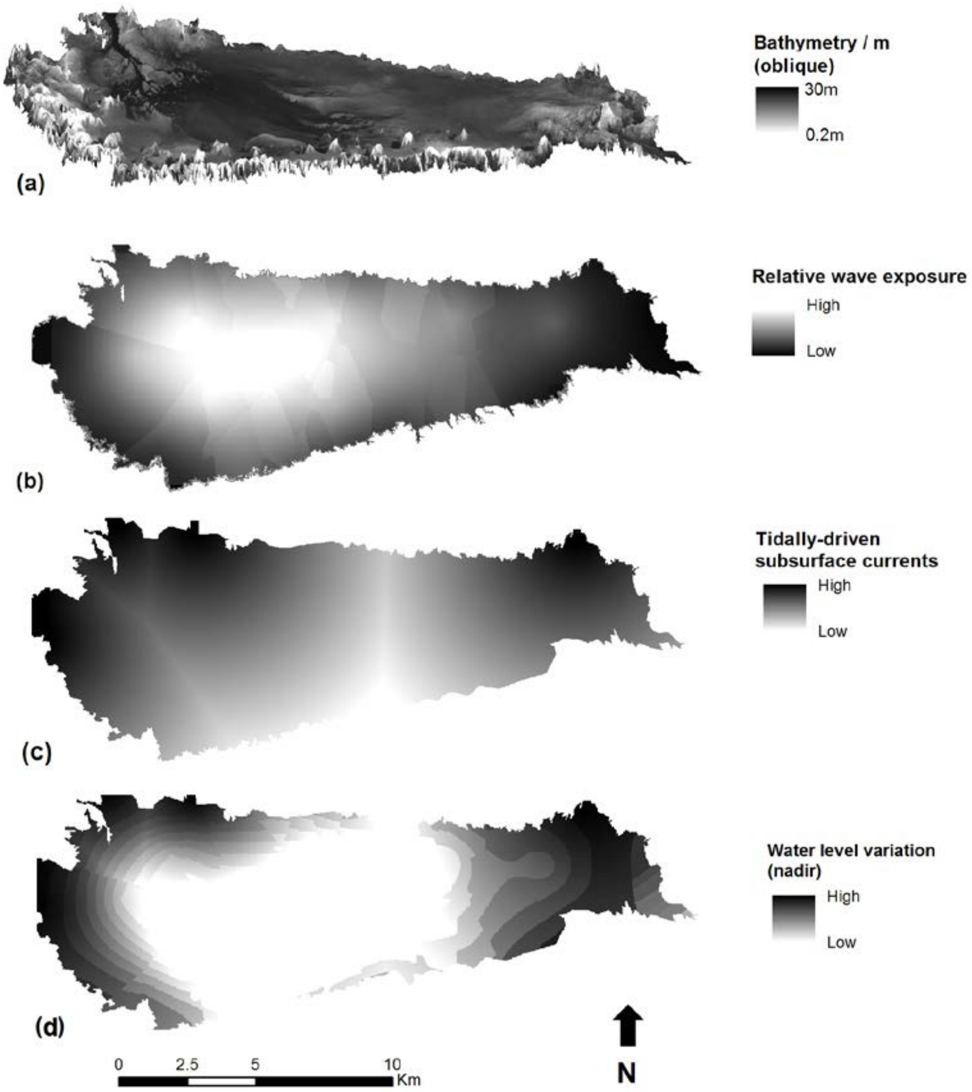

Figure 3. The modelled independent variables (a) lagoon water depth (X_1, Equation (1)) viewed from an oblique angle to emphasise vertical complexity; and (b) water level variation (X_2, Equation (2)) viewed from nadir to emphasise spatial variation across the lagoon.

3.3 Model output

In terms of the distribution of live coral, the ordinary least squares and spatially lagged regression models explained 25% and 79% of the variation of validation points inside the lagoon respectively. For both models, depth was negatively correlated and water level variation was positively correlated with the amount of live coral cover. The residuals from the ordinary least squares regression model displayed strong positive spatial structure, which was corroborated by the Moran Statistic (Figure 4b). For the spatially lagged model, weak negative autocorrelation was apparent (Moran's I ranged from -0.14 to 0.21, Table 3*).*

For the remaining benthic coverages, the spatially lagged autoregressive models consistently performed better than the classic ordinary least squares regression, explaining 81% (carbonate sand), 79% (dead coral) and 72% (macroalgae) respectively of the variation in these components. The independent validation exercise indicated that the spatially lagged models were performing well as benthic cover predictors with the following accuracies: live coral (R^2 0.88), carbonate sand (R^2 0.86), macroalgae (R^2 0.79) and dead coral (R^2 0.84). Water level variation had the highest T-statistic in all cases, apart from that of dead coral cover.

LIVE CORAL: CLASSIC ORDINARY LEAST SQUARES REGRESSION	
R^2 (adjusted value)	0.25 (0.26)
R^2 (validation accuracy)	0.52
Moran's I	0.74
Water depth β Coefficient	-0.08
Water depth T-statistic	-0.02 (p<0.0002)
Water level variation β Coefficient	0.06
Water level variation T-statistic (probability at 2df)	0.03 (p<0.0003)
LIVE CORAL: SPATIALLY LAGGED AUTOREGRESSIVE MODEL	
R^2 (adjusted value)	0.79
R^2 (validation accuracy)	0.88
Moran's I	-0.12
Water depth β Coefficient (standard error)	-0.132
Water depth T-statistic	4.14 (p<0.001)
Water level variation β Coefficient (standard error)	0.381
Water level variation T-statistic (probability at 2df)	8.80 (p<0.001)
CARBONATE SAND: SPATIALLY LAGGED AUTOREGRESSIVE MODEL	
R^2 (adjusted value)	0.81
R^2 (validation accuracy)	0.86
Moran's I	0.21
Water depth β Coefficient (standard error)	0.021 (0.029)
Water depth T-statistic	14.74 (p<0.001)
Water level variation β Coefficient (standard error)	0.248 (0.091)
Water level variation T-statistic (probability at 2df)	27.78 (p<0.001)
MACROALGAE: SPATIALLY LAGGED AUTOREGRESSIVE MODEL	
R^2 (adjusted value)	0.72
R^2 (validation accuracy)	0.79
Moran's I	0.09
Water depth β Coefficient (standard error)	0.054 (0.014)
Water depth T-statistic	13.31 (p<0.001)
Water level variation β Coefficient (standard error)	0.377 (0.112)
Water level variation T-statistic (probability at 2df)	21.13 (p<0.001)
DEAD CORAL: SPATIALLY LAGGED AUTOREGRESSIVE MODEL	
R^2 (adjusted value)	0.61
R^2 (validation accuracy)	0.84
Moran's I	-0.14
Water depth β Coefficient (standard error)	0.145 (0.111)
Water depth T-statistic	12.82 (p<0.001)
Water level variation β Coefficient (standard error)	0.213 (0.073)
Water level variation T-statistic (probability at 2df)	8.04 (p<0.001)

Table 3. Summary of results and diagnostics for each benthic cover class.

The cover of each benthic component predicted by the spatially lagged models closely corresponded to measurements made in the field (R^2 ranged between 0.79 and 0.88). In each case, the spatial distribution of the predicted benthic coverages inside the Aldabra lagoon showed a distinction between areas of the lagoon floor that were in close proximity to the

channels and those at the centre of the lagoon (Figure 4). One area of particular interest was the shallow platform in the northwest quadrant of the lagoon (see Figure 4a), formed by the erosive action of tidally driven currents, which typically reach 3 m s^{-1} on peak ebb tides (Stoddart et al., 1971). For both the ordinary least squares and the spatially lagged models, the predicted distribution of live coral was elevated here, where numerous shallow coral patches were observed in the field (and see also Stoddart et al., 1971; Price 1971: Taylor, 1978; and Potts and Whitton, 1980). Very little live coral was predicted to occur in the south of the lagoon inside the enclosed atoll rim and in the lagoon centre.

The residuals of the ordinary least squares model were spatially structured, with positively autocorrelated residuals occurring in association with Grande Passe and the secondary west and east channel openings (Moran's I = 0.74, see blue patches on Figure 4b). The predicted distribution of carbonate sand was high in the central section of the lagoon and lower around the channel openings at both the east and west margins of the lagoon. Within the central section, sand coverage was highest in the centre of the lagoon. The distribution of macroalgal cover was at its highest inside the channels at the eastern and western margins of the lagoon. Finally, dead coral and rubble were predicted to occur largely in association with live coral, both on the shallow platform to the northeast of the West Channels, and in association with Grande Passe and Passe Houareau (to the east).

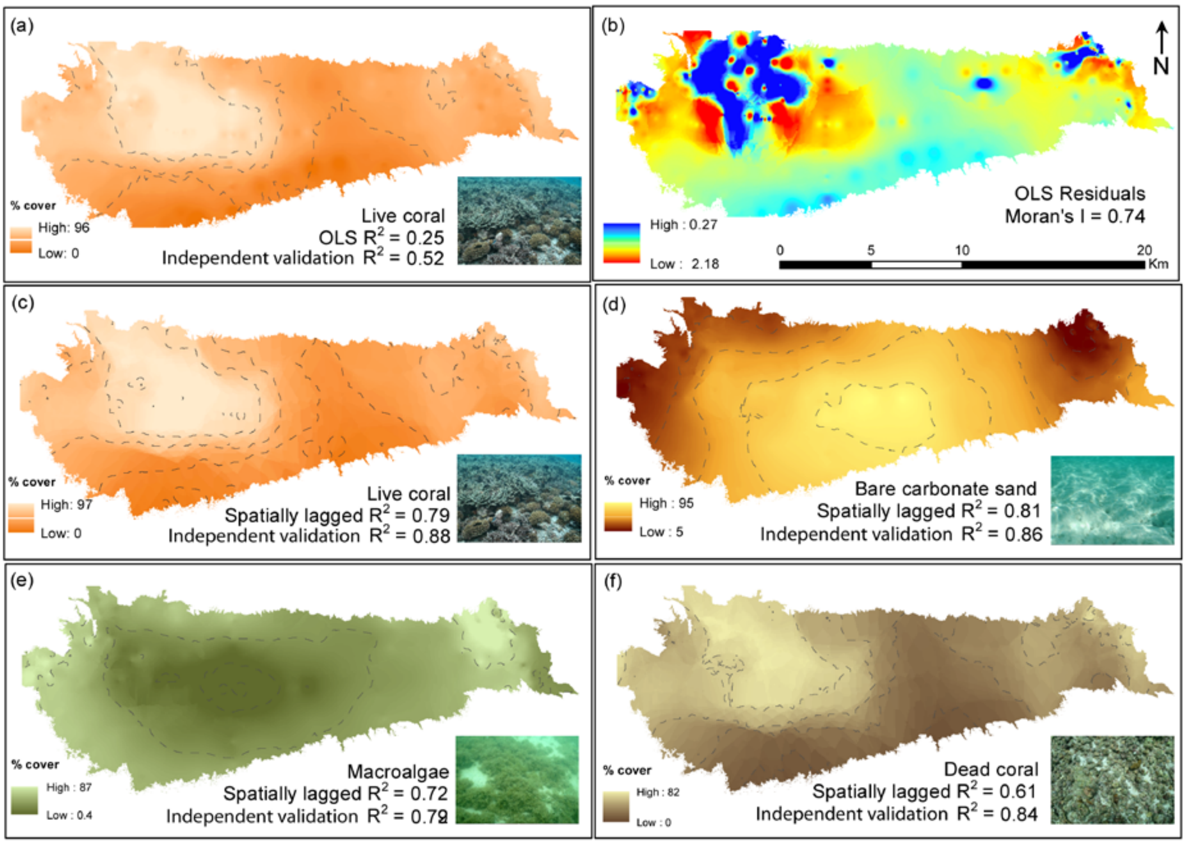

Figure 4. Model output for the different lagoon benthic coverages: (a) Predicted benthic cover of live coral generated from the ordinary least squares (OLS) regression. (b) Standard deviation of the Moran Statistic calculated for the individual data points output from the OLS regression model, and predicted distributions for each of the benthic cover components generated from the spatially lagged autoregressive model. (c) live coral cover; (d) bare carbonate sand cover; (e) macroalgal cover, and (f) dead coral cover. Contours generated for values equivalent to 1, 2 and 3 standard deviations from the mean value for each lagoon benthic cover.

4 Discussion

Taylor (1978) related distinct associations of the molluscan and coral fauna at Aldabra to local sediment characteristics, which themselves reflect variability in hydrodynamic conditions. Inside the lagoon, these were broadly characterised as a "*Porites* coral knoll" assemblage in the northwest and a "*Halimeda* sand" assemblage in the east, with the complexity of hydrodynamic processes around the channels represented by a mosaic of sand, algal and coral habitats. For the western seaward reefs, Price (1971) noted the physiographic response of reef substrate and intertidal vegetation communities to wave action and water depth whereas the blue-green algae communities, occupying around 19% of the intertidal

lagoon area, are largely thought to be controlled by biotic processes including competition and grazing (Potts and Whitton, 1980). The present study extends these previous observations by generating predictions of the spatially continuous coverage of four benthic components (live coral, bare carbonate sand, macroalgae and dead coral) for the whole lagoon. It can be seen from the results of the spatially lagged live coral cover model that the development of live coral stands inside Aldabra Atoll lagoon is highly localised, with the northwestern quadrant emerging as a key site for live coral development on top of a shallow carbonate sandflat (coral coverage ranging from 40 to 60%). This distribution may be due to enhanced wave exposure in this section of the lagoon (Figure 4b), which clearly favours the Porites knoll communities but also particularly provides a favourable environment for the shallow reticulated network of branching Acropora along the northern flank of Grande Passe. It has been suggested for other atoll lagoons (e.g. Tuamotus, Abrolhus and Kiribati), that reticulate and cellular reef development results from self-organisation in coral reefs and is an emergent property of the synergy between rapid lagoonal reef growth and circulation (Blanchon, 2011). This is supported by the video evidence collected in the present study in so far as the video footage taken from the northwestern lagoon quadrant shows a greater degree of reef development than that taken in the east, which relates to smaller, solitary patches of coral. The predicted distribution of dead coral inside the lagoon closely resembles that of live coral, suggesting limited movement of rubble across the shallow sandflat above Grande Passe.

The T-test values suggested that both water depth and circulation were significant predictors of benthic cover ($p<0.001$) and it follows that their contributions to the overall lagoon benthic cover models were valuable; for the spatially lagged models, R^2 ranged from 0.61 – 0.81. This may be because of benthic community components that are reliant on photosynthetic activity, such as coral and algae, for which light interception is closely coupled with water depth

(Finelli et al., 2006). This is particularly the case within the highly enclosed and variable lagoon at Aldabra, where tidal fluctuations and ponding effects result in the differential insolation of shallow platforms. Superimposed onto this, water flow driven by wave stress and tidal currents controls the availability and diffusion rate of nutrients and oceanic plankton biomass to, as well the flushing of particulate matter from, benthic communities inside atoll lagoons (Kraines et al., 2001).

The use of a spatially explicit modelling technique, in which a clear association was maintained and exploited between ground referencing points and the spatial coordinates that located them, enabled autocorrelation of the lagoon benthic assemblages (a widely held property of ecological datasets) to be addressed in a statistically rigorous manner. The initial ordinary least squares model displayed spatial dependence, which may have inflated the goodness of fit measure and underestimated the standard error, increasing the likelihood of a Type I error. Because of this departure from the true independence of observations and failure to include spatial autocorrelation in the specification, some of the effect due to interaction would likely have been allocated to the existing covariates, particularly those with a similar spatial structure to the response variable. Incorporation of a neighbourhood context effect operating through a spatially lagged expression of the response variable allowed this to be addressed. Such a step avoids some of the statistical pitfalls associated with other methods that apply classic regression analysis to generate spatially continuous predictions of benthic character on coral reefs (Garza-Pérez, 2004; McLanahan et al., 2011).

The spatially lagged autoregressive term incorporated information into the model on the response variable itself at sites adjacent to each data point. Any resulting change in predictive power of the model is instructive on the nature (exogenous vs. endogenous) of controls on benthic cover (Cliff and Ord, 1981). It follows therefore, that because the power of the

models was enhanced through the introduction of an autoregressive term, this was attributable to the influence of an endogenous effect acting through a neighbourhood context. Ecological processes underpinning such an effect in an atoll lagoon could include competition for light, larval dispersal and water residence times. Spatially explicit biotic-abiotic relationships inside atoll lagoons such as those empirically defined by the present study can be further tested as predictors of the distribution of macrofaunal lagoon benthic assemblages elsewhere in the Indo-Pacific biogeographic region. In particular, the application of these models may yield insight on the nature of species-environment relationships and potential additional environmental parameters of relevance to lagoons characterised by a different size, shape or water depth. Such an approach applies to the common data scenario for coral reef sites where full coverage information are available on physical variables such as water depth and water level variation, accompanied by point samples of biological communities where field visits were possible.

5 Conclusion

This analysis adds a spatially explicit and statistically rigorous approach to the growing body of bottom-up models used for upscaling local field data to spatially continuous landscapes in an ecologically meaningful manner. Applied for the first time in an atoll lagoon, the species-environment linkages revealed are relevant to similar modelling activities both regionally and globally. A key aim of this study was to establish which type of regression modelling is most appropriate for explaining the distribution of live coral cover inside Aldabra lagoon. To do so, it is useful to distinguish between determinants that reflect endogenous interaction between the sites and those that respond to some other exogenous variable. Assessing the relative contribution of effects caused by a reaction to external forces and effects that are a reaction to neighbouring individuals determines the appropriateness of the model specified. When external forces are the major influence, a classic ordinary least squares regression model is appropriate, whereas interactive effects suggest a need for a model with a spatially dependent

covariance structure (Cliff and Ord, 1981). Transition to a model that incorporated spatial dependence was accompanied by a marked growth in predictive power (in the example of live coral, R^2 increased from a value of 0.25 to 0.79). The theoretical implication that follows is that neighbourhood interactions play an important role in defining lagoon benthic character. This invites greater consideration of interaction between sites, providing a persuasive case for explicitly building geographical considerations into ecological studies of benthic cover classes inside atoll lagoons. Finally, the application of such techniques has value for focusing conservation and resource management activities, both in a geographical and thematic sense. For example, the output is expressed on a ratio scale, which represents a high measurement level that can be utilised (through contouring or the application of thresholds) to identify a set of representative locations in line with established conservation objectives (Roberts et al. 2003).

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