Spatial interpolation of the sessile community of Madagascar reef, Gulf of Mexico (#9390)

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Spatial interpolation of the sessile community of Madagascar reef, Gulf of Mexico

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Information about the distribution and abundance of the habitat-forming sessile organisms in marine ecosystems is of great importance for conservation and natural resource managers. Spatial interpolation methodologies can be useful to generate this information from *in situ* sampling points; especially in circumstances where remote sensing methodologies ~~can not~~ be applied due to small scale spatial variability of the natural communities and low light penetration in the water column. Interpolation methods are widely used in environmental sciences; however, published studies using these methodologies in coral reef science are scarce. We compare the accuracy of the two most commonly used interpolation methods in all disciplines, inverse distance weighting (IDW) and ordinary kriging (OK), to predict the distribution and abundance of hard corals, octocorals, macroalgae, sponges and zoanthids and identify hotspots of these habitat-forming organisms in Madagascar reef, one of many reefs located on the Yucatan continental shelf that have been poorly studied despite being important centers of biodiversity and fishery resources. IDW and OK generated similar distribution patterns for all the taxa; however, crossvalidation tests showed that IDW outperformed OK in the prediction of their abundances. Despite its greater complexity, OK had higher mean prediction errors and failed to correctly interpolate the highest abundance values measured *in situ*, with the exception of macroalgae, whereas IDW had lower mean prediction errors and high correlations between predicted and measured values in all cases. The deeper sandy environments of the leeward and windward regions were dominated by macroalgae, seconded by octocorals. However, the shallow rocky environments of the reef crest had the highest richness of habitat-forming groups of organisms; here, we registered high abundances of octocorals and macroalgae, ~~but~~ sponges, *Millepora alcicornis* and zoanthids ~~dominated~~ in some patches, creating high levels of habitat heterogeneity that could benefit many mobile species. The accurate spatial interpolations created using IDW allowed us to see the spatial variability of each

taxa at a biological and spatial resolution that remote sensing would not have been able to produce. Our study sets the basis for further research projects and conservation management in Madagascar reef and encourages similar studies in the region and other parts of the world where remote sensing technologies are not suitable for use.

Spatial Interpolation of the Sessile Community of Madagascar Reef, Gulf of Mexico.

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ABSTRACT

Information about the distribution and abundance of the habitat-forming sessile organisms in marine ecosystems is of great importance for conservation and natural resource managers. Spatial interpolation methodologies can be useful to generate this information from *in situ* sampling points; especially in circumstances where remote sensing methodologies can not be applied due to small scale spatial variability of the natural communities and low light penetration in the water column. Interpolation methods are widely used in environmental sciences; however, published studies using these methodologies in coral reef science are scarce. We compare the accuracy of the two most commonly used interpolation methods in all disciplines, inverse distance weighting (IDW) and ordinary kriging (OK), to predict the distribution and abundance of hard corals, octocorals, macroalgae, sponges and zoanthids and identify hotspots of these habitat-forming organisms in Madagascar reef, one of many reefs located on the Yucatan continental shelf that have been poorly studied despite being important centers of biodiversity and fishery resources. IDW and OK generated similar distribution patterns for all the taxa; however, crossvalidation tests showed that IDW outperformed OK in the prediction of their abundances. Despite its greater complexity, OK had higher mean prediction errors and failed to correctly interpolate the highest abundance values measured *in situ*, with the exception of

macroalgae, whereas IDW had lower mean prediction errors and high correlations between predicted and measured values in all cases. The deeper sandy environments of the leeward and windward regions were dominated by macroalgae, seconded by octocorals. However, the shallow rocky environments of the reef crest had the highest richness of habitat-forming groups of organisms; here, we registered high abundances of octocorals and macroalgae, but sponges, *Millepora alcicornis* and zoanthids dominated in some patches, creating high levels of habitat heterogeneity that could benefit many mobile species. The accurate spatial interpolations created using IDW allowed us to see the spatial variability of each taxa at a biological and spatial resolution that remote sensing would not have been able to produce. Our study sets the basis for further research projects and conservation management in Madagascar reef and encourages similar studies in the region and other parts of the world where remote sensing technologies are not suitable for use.

INTRODUCTION

Coral reefs are important centres of biodiversity (Plaisance *et al*., 2011) that provide multiple natural resources ~~to the human societies~~ (Mumby *et al*., 2011). However, multiple disturbances are impacting these ecosystems and causing changes in their community structure (Norström *et al*., 2009). The main groups of sessile organisms inhabiting coral reefs are hard corals (scleractinian and millepores), macroalgae, octocorals, sponges, and zoanthids (Lewis, 2006; Diaz & Rützler, 2001; Norström *et al*., 2009; Wee *et al*., 2017); these taxa are habitat-forming organisms (HFO) that shelter many species of fishes, echinoderms, gastropods, mollusks and crustaceans (Duffy 1992, Goh, Ng & Chou, 1999; Pérez *et al.*, 2005; Santavy *et al*., 2013; Cházaro-Olivera & Vázquez-López, 2014), which in turn sustain the fisheries and tourism industries of the world (Moberg & Folke, 1999). ~~Traditionally, h~~ard corals used to dominate the seascape of tropical reefs; however, their populations have declined ~~since decades ago~~ due to multiple disturbances such as overfishing, eutrophication and high temperatures (Nystrom & Folke, 2001), allowing other HFO to increase their abundances (Nyström, Folke & Moberg, 2000; Wilkinson, 2004; Ruzicka *et al*., 2013; McMurray, Finelli & Pawlik, 2015). Many coral reefs are now dominated by macroalgae (McManus & Polsenberg, 2004), with other reefs presenting high percentages of substrate covered by octocorals, zoanthids and sponges (Norström

et al., 2009; Cruz *et al*., 2014; Bell *et al*., 2013). Although~~, there is uncertainty~~ about the specific ecological changes that may take place in the future, it is very likely that ~~these transitions~~ will continue as global warming intensifies (Bell *et al*., 2013; Gross, 2013; Ruzicka *et al*., 2013). Most ecological studies have lacked a community perspective and have focused on just a couple of taxonomic groups, mainly scleractinian corals and macroalgae (McManus & Polsenberg, 2004). However, as the community structure of coral reefs transitions, the need to monitor the distribution and abundance of all HFO has increasingly received more attention (Norström *et al*., 2009; Bell *et al*., 2013; Ruzicka *et al*, 2013; McMurray, Finelli & Pawlik, 2015).

The assessment of the abundance of all HFO is important; however, ~~its inclusion into~~ geographic information systems (GIS) is needed for scientific, conservation and resource management organizations, since this allows the planning of monitoring programs and establishment of conservation areas (Franklin *et al*., 2003; Lee *et al*., 2015). Much research about the spatial distribution of the sessile benthic communities in reef ecosystems has focused on remote sensing (Kachelriess *et al*., 2014). Remote sensing technologies allow the assessment of the distribution of marine sessile organisms in extensive areas following complex procedures (Mumby *et al.,* 1998). However, ~~its~~ accuracy diminishes as water turbidity and depth increases because of the light absorption by the water column (Lucas & Goodman, 2014). In addition, ~~its ability~~ to identify different taxa and accurately estimate i[illegible]undance is limited (Kutser & Jupp, 2006) and the coarse spatial resolution of the images may not match the natural patchy variation of the sessile communities (Andrefouet *et al.,* 2003; Kachelriess *et al*., 2014), requiring ~~an~~ *in situ* verification of the remote sensing estimations (ground-truthing), which ultimately add extra costs and effort to the studies (Botha *et al.,* 2013; Lucas & Goodman, 2014). ~~Thus, b~~y now these procedures are only ideal for macro-scale studies of reefs located in clear and shallow water environments (*e.g*. Zapata-Ramirez *et al.,* 2014). However, there are many coral reefs around the world ~~with~~ relatively small sizes (*e.g.* ~1 km^2), ~~having deep habitats~~ and/or developing under turbid environments, many of which are of conservation priority (Cohen & Foale, 2013). ~~For~~ these cases, species distributions and abundance estimated through spatial interpolations based entirely on data gathered *in situ* may be more appropriate, since they do not have depth, water clarity or spatial scale limitations and can be integrated into GIS (McClanahan *et al.,* 2011; Walker *et al.,* 2012; D'Antonio *et al.,* 2016).

There are many spatial interpolation methodologies used to predict the distribution of variables of interest in different disciplines (Li & Heap, 2008). Among them, kriging, a geostatistical methodology, and inverse distance weighting (IDW), a simpler non-geostatistical methodology, have been used widely to predict many environmental and agricultural variables (reviewed by Li & Heap, 2008, 2011, 2014), such as soil fertility (Mueller *et al.,* 2004), mud content (Li *et al*., 2011) and bathymetry (Bello-Pineda & Hernández-Stefanoni, 2007). Published studies in marine ecology applying these methods to generate distribution and abundance maps of marine organisms are less common. Kriging has been used for crustaceans (Rufino *et al*., 2005, Surette, Marcotte & Wade, 2007), echinoderms (Hernandez-Flores *et al.,* 2015), fish (Rueda & Defeo 2003, De Mazières & Comley, 2008; Ruppert *et al.,* 2009), seagrass (Holmes *et al*., 2007), hard corals and encrusting algae (Knudby *et al.,* 2013); whereas studies using IDW have been limited to mollusks (Berry, Hill & Walker, 2016), coral cover (Walker *et al.,* 2012; D'Antonio *et al.,* 2016), coral diameters (Burman, Aronson & Woesik, 2012) and coral and fish diversity (McClanahan *et al.,* 2011). However, no study has applied these two methodologies across different HFO.

The Gulf of Mexico has many important reef systems that have been studied extensibly (Chávez, Tunnell & Withers, 2007; Hickerson *et al.,* 2008; Horta-Puga *et al.,* 2015); Nonetheless, many other smaller reefs located on the Yucatan continental shelf and developing on turbid waters lack information about their physical and biological characteristics, despite being important centers of biodiversity and fishery resources (Zarco-Perello *et al.* 2013). The present study (i) gathered baseline information of the abundance of all HFO inhabiting one of these poorly studied reefs, (ii) described its community structure, (iii) compared the accuracy of IDW and OK to interpolate their abundances and (iv) synthesize this information creating a map of the HFO richness in the reef.

MATERIALS AND METHODS

Sampling design

15 photo-transects 200 m long, separated 200 m from each other and distributed along the whole extent of Madagascar reef (Zarco-Perello, Moreno-Mendoza & Simoes, 2014) were done from August to October of 2007 (Fig. 1). Photo-quadrats (0.8m^2) of the benthos were taken every 5 m along the transects, each one representing a sampling point (n = 580). Information about geographic coordinates, depth, substrate type (*i.e.* rock, sand and rubble) and reef region (*i.e.* windward, crest and leeward) of each sampling point was recorded.

Community structure analyses

Abundance (*i.e.* percent cover) of all the HFO was calculated in each photograph using the point-count method (see Fabricius & McCorry, 2006 and Ruzicka *et al.,* 2013). Biological similarities between the different regions of the reef were analyzed with non-metric Multi-Dimentional Scaling (nmMDS) and an Analysis of Similarity (ANOSIM) to test for statistical significance; data was log transformed and the distance matrix was calculated with the bray-curtis method using the software R v.3.1.3 (vegan package) (The R Foundation) with the interphase RStudio v.0.99.473 (Rstudio, Inc.).

Spatial interpolation analyses

The spatially referenced percent cover data of each photography was used to interpolate the abundance of each HFO using IDW and Ordinary Kriging (OK), the most recommended univariate method of kriging (Li & Heap, 2014). IDW and OK interpolations are based on the principle of spatial autocorrelation of samples by distance, where the closer the samples are of each other, the more similar would be their values. Under this principle, the prediction of a value in an unsampled place is calculated by giving more weight to samples that are closer to the prediction point. However, IDW uses arbitrary exponential weighting of the influence that each sample has according to distance, whereas OK involves a process of variography to model the spatial autocorrelation of the data to assign weights, this can result in better interpolations under an appropriate sampling design; nonetheless it is time consuming and it is still subjective since it involves many user decisions (Li & Heap, 2014). Finally, both interpolators use a determined quantity of observations for the predictions; this observations must be located within a ‘searching

window', an area around the point of prediction, which geometry is defined by the user based on the empirical knowledge of the phenomena under study (Li & Heap, 2014).

~~Before the predictions,~~ our biological datasets were randomly separated in half: training and test datasets. OK and IDW models were created using the training dataset. For OK, the models (*e.g.* spherical and exponential) that best fitted the data of the variograms of each HFO were selected; for IDW, different power values (*i.e.* 1, 2, 3) were used as weighting factors for each HFO. The parameters of searching window were the same for both methodologies. The best models of OK and IDW for each HFO were selected following cross-validations based on the test dataset (Goovaerts, 1997; Supplementary Information). The performance of both methodologies was compared based on the mean error of their predictions, the regression coefficient (r^2) of predicted against measured values, graphical comparisons (box-plots) of the distribution of predicted and measured data and visual examination of the predicted maps (Hernandez-Flores *et al.,* 2015). ~~T~~he interpolation map of hard corals ~~was done~~ only with data of *Millepora alcicornis* (millepora) since the inclusion ~~in the model~~ of scleractinian corals produced overestimations ~~on the predictions~~ given the small colony sizes found *in situ* (< 25 cm^2).

The descriptions of the spatial patterns of all HFO were based on the interpolated abundance maps of the best performing methodology (OK vs IDW). These interpolated maps were transformed to rasters (5 m resolution) and reclassified to presence/absence with the same resolution. These rasters were used to create a map of the HFO richness on the reef by summing all the HFO present in each cell (0 to 5 scale). The spatial interpolation analyses were done using the software ArcMap v.10.3 with the Geostatistical and Spatial Analyst extensions (ESRI corp.).

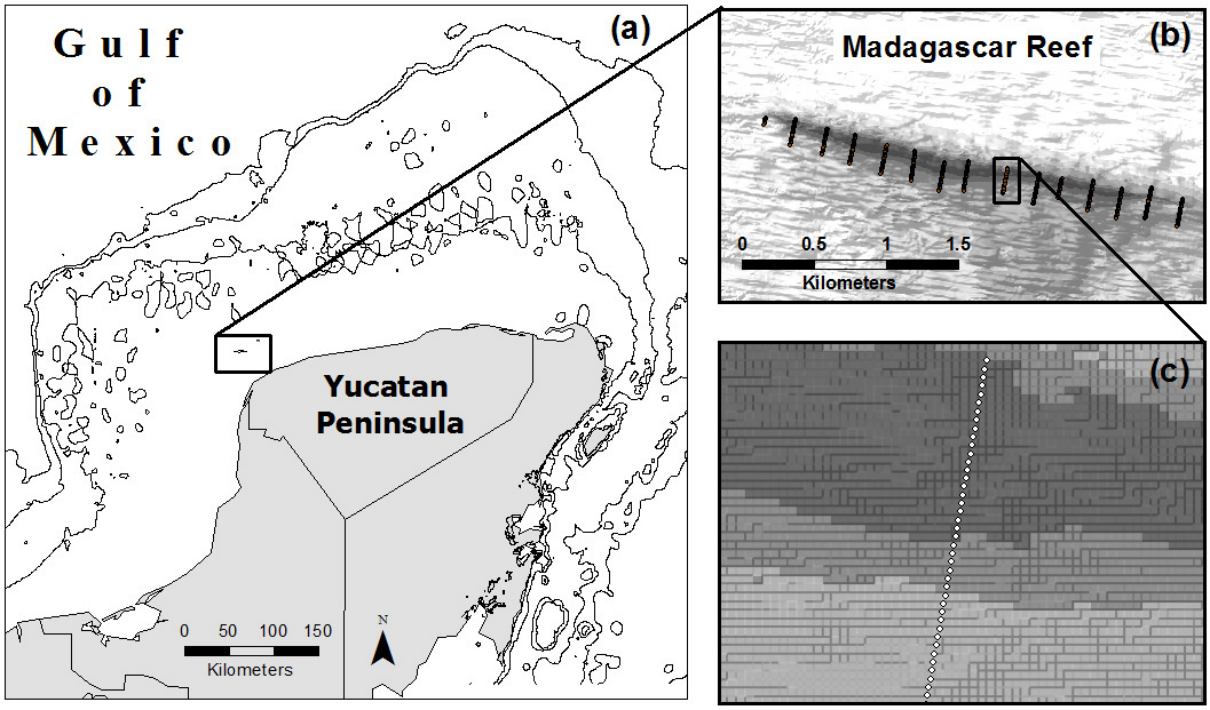


Figure 1. Localization of Madagascar reef in the Gulf of Mexico (a) and distribution of sampling points across the bathymetric gradient along the reef (b, c).

RESULTS

Community Structure

The sessile community of Madagascar reef differentiated spatially between the reef crest and the windward and leeward regions. The nmMDS showed two statistically significant different clusters, one belonging to sampling units from the reef crest and another one belonging to the leeward and windward regions (ANOSIM, p= 0.001) (Fig. 2). The reef crest presented all HFO, whereas the windward and leeward regions were greatly dominated by macroalgae, with octocorals in a lower magnitude (Fig. 3).

The reef crest, ~~being~~ the shallower region of the reef (depth: 6.8 ± 1.4 m) ~~and presenting rocky substrate~~, had the higher average abundances of hard corals (3.7 %), zoanthids (7.7 %) and sponges (7.0 %), with octocorals (44.0 %) and macroalgae (37.4 %) dominating the reefscape

(Fig. 4)~~; as~~ depth increased towards the windward (depth: 16.2 ± 2.6 m) and leeward regions (depth: 14.8 ± 0.16 m) so did the sandy substrate and the abundance of macroalgae, whereas the abundance of all the other sessile groups decreased (Fig. 4)~~; m~~acroalgae covered 80% of the substrate in each ~~of them,~~ followed by octocorals ~~covering 9% at the windward and 14 % at the leeward region~~ (Fig. 4). Hard corals, sponges and zoanthids were scarce in these environments but had slightly higher abundances at the windward (2.6%, 1.0% and 0.7 % respectively) than at the leeward region (1.4 %, 0.8% and 0% respectively) (Fig. 4). Scleractinian corals had low abundances in general but were more abundant at the windward and leeward regions (0.7%) than at the reef crest (0.1%).

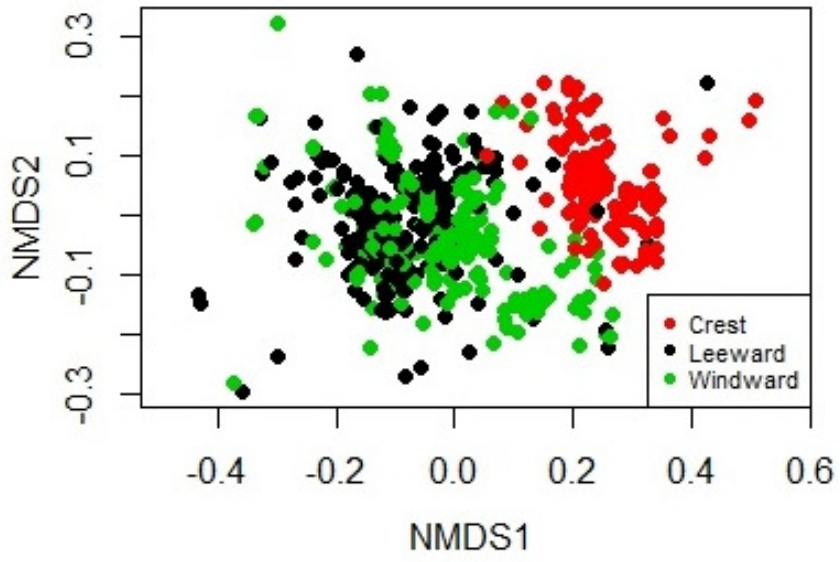
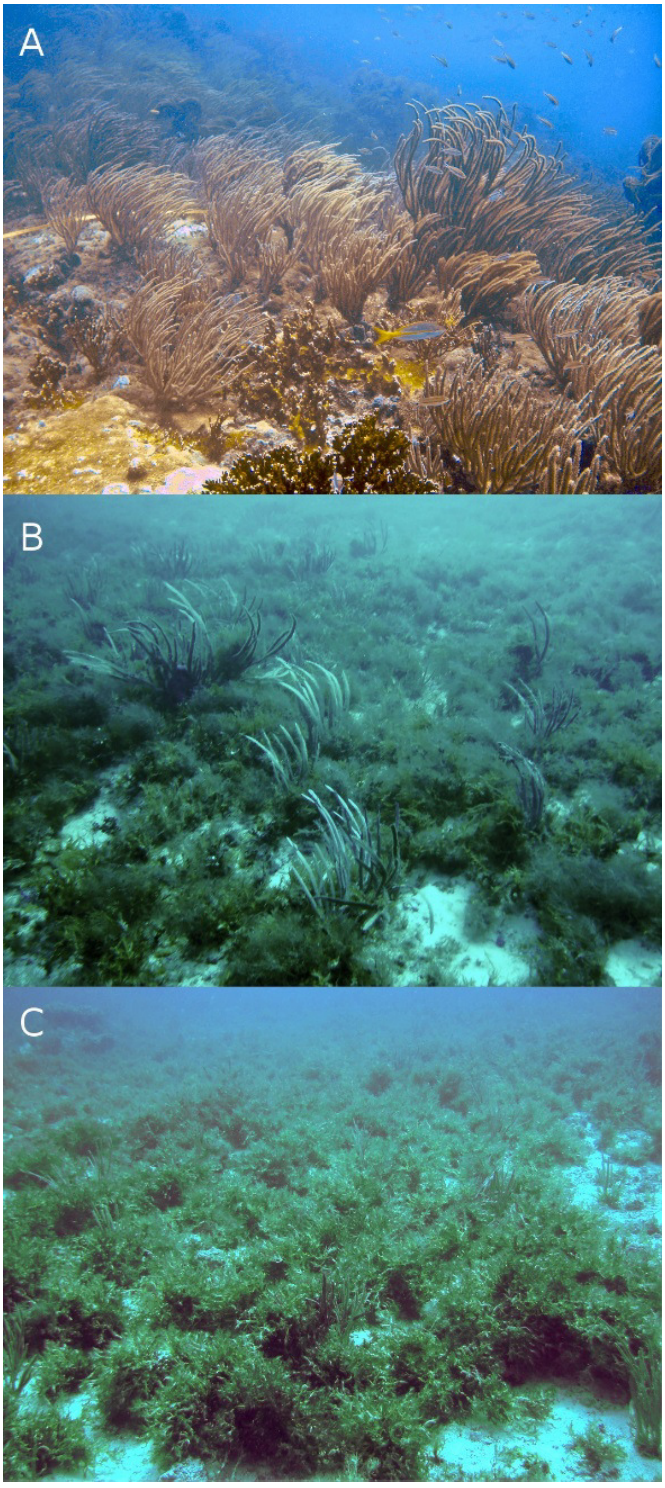


Figure 2. Non-metric Multidimensional Scaling biplot showing the similarity on the biological composition between sampling units taken at the windward, reef crest and leeward zones of Madagascar reef, Gulf of Mexico.



206

207 Figure 3. Typical reefscapes of Madagascar reef, Gulf of Mexico: The shallow (depth: 6.8 ± 1.4 m) rocky
208 reef crest (A), and the deeper sandy leeward (14.8 ± 0.16 m) (B) and windward (16.2 ± 2.6 m) (C)
209 regions.

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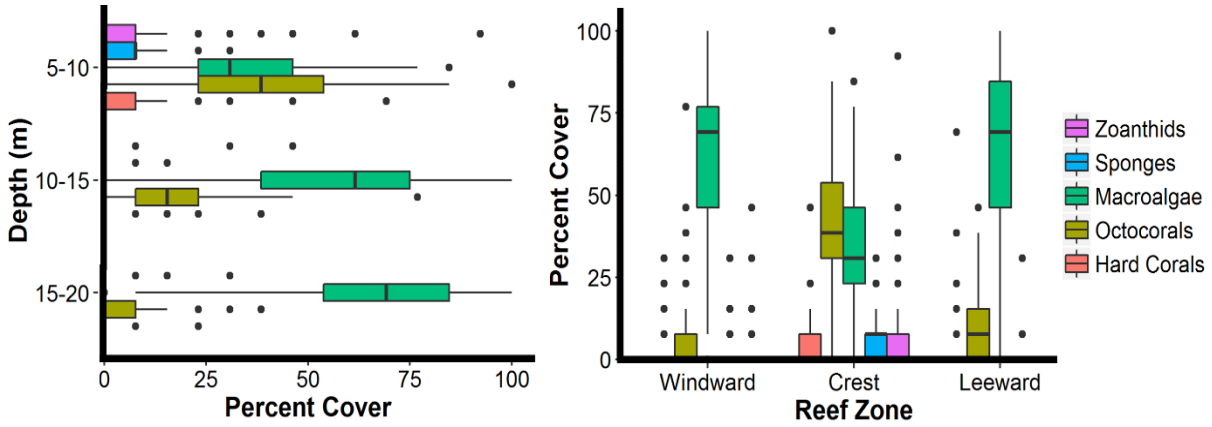


Figure 4. Relative abundance of the main groups of sessile organisms at different depth intervals and zones of Madagascar reef, Gulf of Mexico. Box-plots represent four quartiles and median, with outliers as points.

Spatial interpolations

The OK and IDW produced similar interpolation maps, capturing the same patterns of distribution and abundance of each HFO with no anomalies detected on the maps generated by each methodology. However, IDW outperformed OK in the accuracy of the abundance values interpolated. IDW presented lower mean errors than OK in the ~~crossvalidation~~ of all HFO, with the exception of macroalgae, and had higher ~~r^2~~ values on all the interpolations (Table 1); OK had low values of r^2 for millepora, zoanthids and sponges (Table 1). Similarly, the distributions of the interpolated data of IDW had a higher resemblance to the measured values than those generated with OK for each HFO (Fig. 5). IDW was a good predictor of the highest values of abundance measured *in situ* for all HFO, whereas the predictions of OK fell short on octocorals, sponges, zoanthids and millepora (Fig. 5).

Table 1. Mean error (ME) of the predicted interpolations and regression coefficients (r^2) between predicted and measured values by Inverse Distance Weighting (IDW) and Ordinary Kriging (OK) of the main habitat-forming organisms (HFO) of Madagascar reef, Gulf of Mexico.

HFO	IDW		OK	
	ME	r^2	ME	r^2
Millepora	0.00001	0.938	0.00003	0.549
Zoanthids	0.00005	0.989	0.0001	0.437
Sponges	0.0000004	0.957	0.00006	0.732
Octocorals	0.0001	0.971	0.0004	0.852
Macroalgae	0.0006	0.957	0.0003	0.824

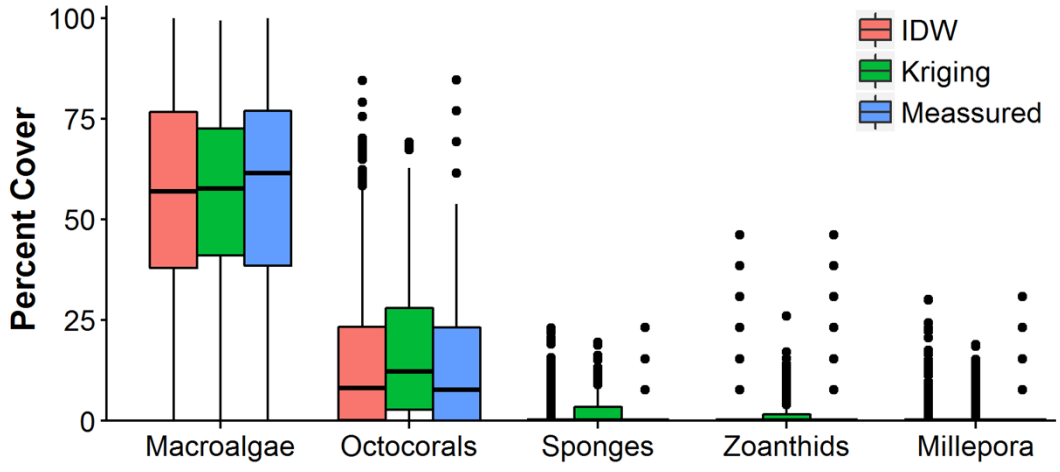
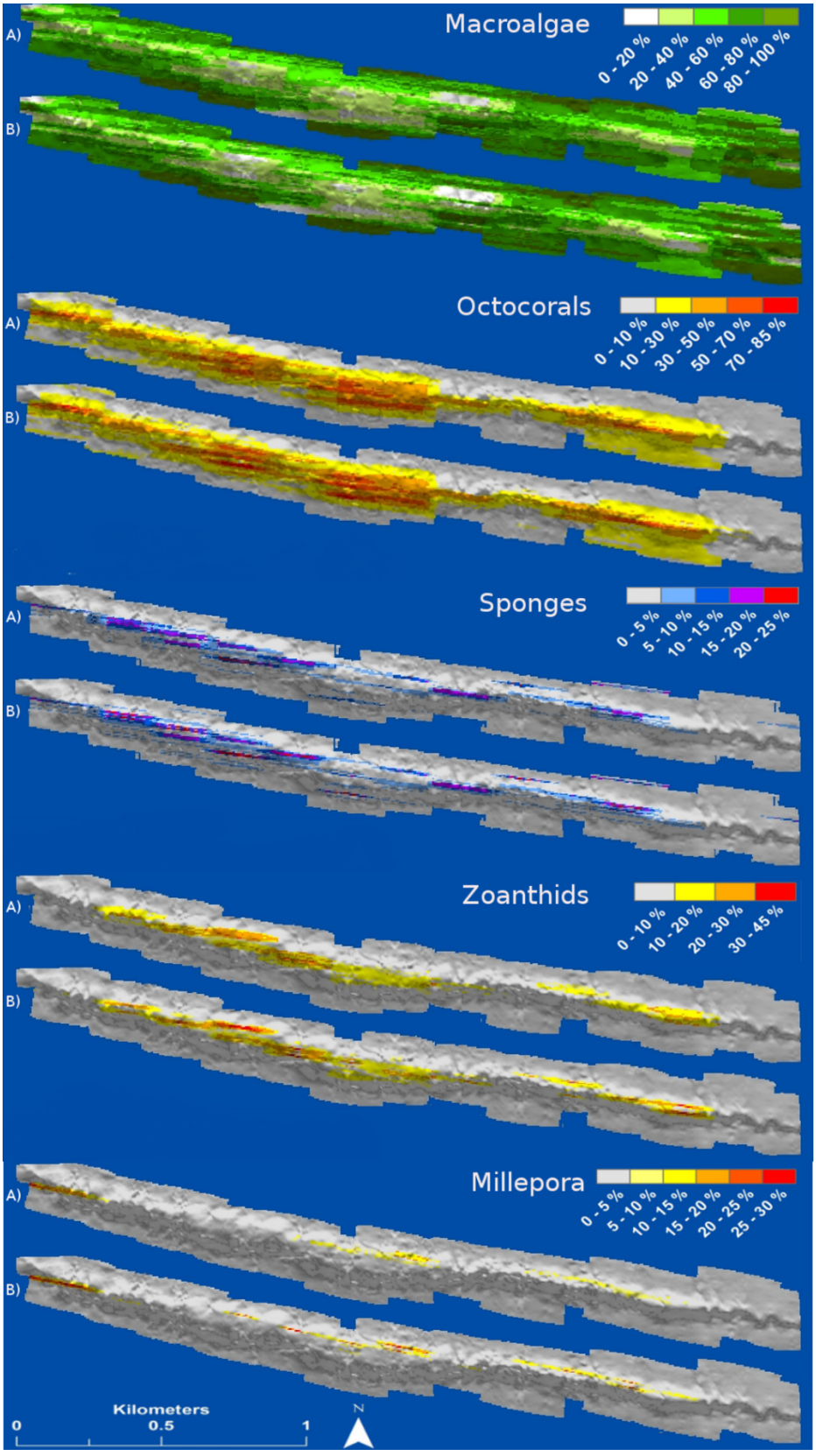


Figure 5. Comparison of the abundance values measured *in situ* of macroalgae, octocorals, sponges, zoanthids and *Millepora alcicornis* of Madagascar reef, Gulf of Mexico, and those interpolated by Inverse Distance Weighting (IDW) and Ordinary Kriging during crossvalidation. Box-plots represent four quartiles and median, with outliers as points.

The interpolation maps presented detailed information of the distribution and abundance of each HFO. The spatial distribution of all HFO was patchy, with specific areas of the reef presenting higher abundances. Macroalgae were distributed in all regions of the reef but were more abundant in deeper areas at the windward and leeward regions, where they covered up to 100% of the substrate (Fig. 6). Octocorals covered extensive areas of the reefscape as well, but patches at the central and western reef crest had higher abundances, where they covered up to 85% of the substrate (Fig. 6). Sponges were mainly distributed all along the reef crest, with patches at the western side presenting higher abundances (25%), but there were also isolated colonies in deeper

252 zones (Fig. 6). Zoanthids presence was limited to the reef crest, where patches at the west and
253 east sides covered up to 45% of the substrate; at the center-eastern side of the reef their
254 distribution was interrupted, in this gap macroalgae and octocorals had high abundances (Fig. 6).
255 Millepora distribution was the most restricted and covered the smallest total substrate area of the
256 reef among all the HFO; colonies were distributed in three disconnected areas of the reef crest, at
257 the western, center and eastern regions, each presenting patches covering up to 30% of the
258 substrate (Fig. 6); the space gaps between areas of millepora had high abundances of the rest of
259 the HFO (Fig. 6).


Macroalgae
0 - 20 %
20 - 40 %
40 - 60 %
60 - 80 %
80 - 100 %
Octocorals
0 - 10 %
10 - 30 %
30 - 50 %
50 - 70 %
70 - 85 %
Sponges
0 - 5 %
5 - 10 %
10 - 15 %
15 - 20 %
20 - 25 %
Zoanthids
0 - 10 %
10 - 20 %
20 - 30 %
30 - 45 %
Millepora
0 - 5 %
5 - 10 %
10 - 15 %
15 - 20 %
20 - 25 %
25 - 30 %
A)
B)
Kilometers
0
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1
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Figure 6. Maps of fistribution and abundance (percent cover) generated by kriging (A) and inverse distance weighting (B) of the main groups of hábitat-forming organisms of Madagascar reef, Gulf of Mexico.

HFO richness had a positive relationship with depth (Fig. 7). Deep sandy areas at the windward and leeward regions had values of 1, ~~having only macroalgae~~; slightly shallower areas, where octocorals were more common had values of 2. Only the reef crest had extensive areas with values of 3 and 4, where either *M. alcicornis*, sponges and zoanthids were present in addition to macroalgae and octocorals. Three areas with the highest richness levels were localized at the shallowest regions of the reef crest, one at the east and two on the west side (Fig. 7).

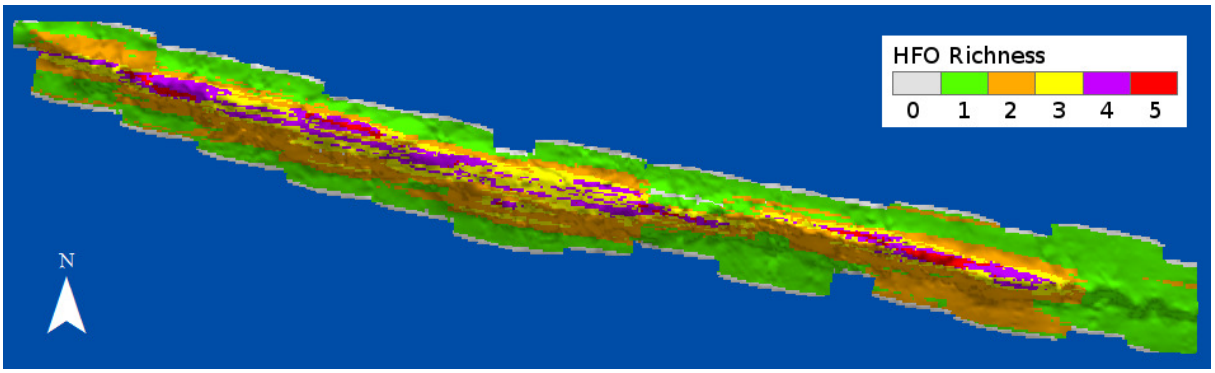

Figure 7. Richness of habitat-forming organisms (HFO) in Madagascar reef, Gulf of Mexico. The calculation considers the presence of macroalgae, octocorals, sponges, zoanthids and *Millepora alcicornis*.

DISCUSSION

Community structure

Madagascar reef sessile community ~~distinguishes~~ from other reefs of the Gulf of Mexico. ~~T~~he windward and leeward regions of the reefs at the Campeche Bank Reef System, Veracruz Reef System and Tuxpan Reef System have been described as having important abundances of scleractinian corals (Chávez, Tunnell & Withers, 2007; Larson *et al*., 2014; Horta-Puga *et al.,* 2015); however, we ~~found~~ very small colonies and ~~thus~~ very low abundance of scleractinian corals~~, only~~ the hard coral *M. alcicornis* was conspicuous at the reef crest, while the leeward and

windward regions were dominated by macroalgae. Our results also contrasted with reef systems further North, at the Flower Garden Banks, where surveys have reported high abundances of scleractinian corals (>50%) and low substrate cover (<1%) of other sessile organisms, ~~excepting Stetson Bank that had high abundances~~ of *M. alcicornis* (30%) and sponges (30%) (Hickerson *et al.,* 2008). Madagascar reef crest was dominated by octocorals and macroalgae, but sponges and zoanthids were very conspicuous in different patches of the reef. Studies in the Caribbean have reported abundances of sponges as high as 24% in shallow environments (Diaz & Rützler, 2001), we found a lower average abundance at the reef crest (7%); however, substrate cover reached 25% in some areas. Millepores usually cover < 10% of substrate over entire reefs but can be abundant in localized regions (Lewis, 2006), *M. alcicornis* covered ~3% on average in Madagascar reef but in its more important areas of distribution its abundance reached 30%. Zoanthids can have high abundances in shallow environments; reefs in Brazil had ~ 6% substrate covered on average (Silva *et al.,* 2015) with 25% in localized areas (Francini-Filho *et al*., 2013)~~,~~ ~~reefs at St. Croix~~ had 36% (Suchanek & Green, 1981) ~~and intertidal flats of the Southern Caribbean can have ~50%~~ (Belford & Phillip, 2012; Rabelo *et al.,* 2015)~~; our data fell within these numbers, zoanthids covered 7.7% on average but reached 45% in its core distribution areas~~. Octocorals are a common element in reefs of the Gulf of Mexico, Caribbean (Jordan-Dahlgren, 2002) and other coral reefs of the world (Fabricius & McCorry, 2006). ~~h~~owever, ~~abundances~~ can vary widely~~,~~ ~~studies~~ in the Gulf of Mexico and Caribbean have reported low abundances (2%) ~~in Cuba~~ (Chiappone *et al*., 2001), moderate abundances (~ 16%) ~~at~~ the Florida Keys (Ruzicka *et al*., 2013) and ~~very~~ high abundances (54%) ~~at~~ the Enmedio reef in Veracruz, Mexico (Nelson, Stinnett & Tunnell, 1988). ~~Worldwide, some reefs at~~ the Great Barrier Reef in Australia ~~have presented~~ an average of 20% cover (Fabricius, 1997)~~, while unusual abundances have been reported~~ in New Guinea (40%) (Tursch & Tursch, 1982) and the Red Sea (50%) (Benayahu & Loya, 1981). Our results ~~are similar~~ to the highest values reported regionally and globally: 44% on average with 85% substrate covered on extensive areas of the reef crest. On the other hand, the high cover of macroalgae on all environments of the reef is not extraordinary~~,~~ ~~since~~ this group has become dominant in many coral reef regions of the world (Arias-Gonzalez *et al.,* 2017).

Spatial interpolations

IDW seems a very promising methodology for the interpolation of the abundance of the main HFO inhabiting coral reefs. Kriging and IDW are the most widely used interpolation methods in all disciplines, and kriging is generally considered a better interpolator (Li *et al.,* 2011); however, our results showed that IDW can generate more reliable predictions for all HFO. OK interpolations generated successful maps of macroalgae and octocorals, but the interpolations for *M. alcicornis,* sponges and zoanthids fell short of the highest values measured *in situ* as shown in the crossvalidaton. Despite this, the OK interpolations represented the distributions correctly and could allow the creation of presence/absence data, which is a common expression of abundance in ecology (Royle & Nichols, 2003). However, IDW ~~got~~ lower mean errors and higher r^2 ~~on the crossvalidations~~ because ~~its~~ predictions did not underestimate the values gathered *in situ*. Other studies have found similar results, where kriging is not able to predict the highest values of the measured data (Hernandez-Flores *et al*., 2015) and IDW outperforms kriging interpolators; Gong *et al.* (2014) found that IDW was the best interpolator for arsenic concentrations in comparison with kriging, Spokas *et al*. (2003) concluded that IDW performed best for methane flux, and Wartenberg *et al*. (1991) concluded that kriging was not superior to non-geostatistical methods at interpolating groundwater contamination despite its greater complexity. Many ecological studies in the past have assessed the abundance of different HFO, but have not presented the information in a clear spatially explicit fashion (*e.g.* Newman *et al.,* 2006; Ruzicka *et al.,* 2013). This is an important aspect in modern ecology that should be a standard procedure in studies regarding community structure of marine ecosystems; we show that this can be done accurately using a simple interpolation methodology.

The interpolations allowed us to see the precise spatial patterns of distribution and abundance of each HFO. Non-spatial analyses summarize ecological data and give general trends of abundance through statistical graphics (*e.g.* boxplots); however, without geographic coordinates ~~this does~~ not describe the spatial patterns precisely, ~~hiding~~ macro-ecological processes. Our interpolations showed how the ~~space~~ of the reef was distributed among all the HFO in a mosaic fashion. Each HFO had particular areas of high ~~abundances~~ at the reef crest, suggesting that despite the general dominance of octocorals and macroalgae there is ~~an~~ ongoing strong competition for space. All the HFO are strong competitors (Wulff, 2006; Lewis, 2006; Rabelo, Soares & Matthews-Cascon,

2013; Sebens & Miles, 1988; Fong & Paul, 2011; Cruz *et al*., 2016) and can influence the distribution and abundance of ~~each other~~ by means of physical and chemical mechanisms that alter individual colonies and demographic processes of whole populations (Chadwik & Morrow, 2011).

The higher HFO richness and competition among the sessile groups at the reef crest seems to be related to depth and substrate type. The rocky substrate of the reef crest allows the recruitment of individuals from all the HFO (Kinzie, 1973) and the expansión of colonies through asexual reproduction (Jackson, 1977). In contrast to the unstable sandy substrate of the windward and leeward regions that benefit macroalgae due to their high propagation capacities, faster growth rates and substrate attachment through rhizoids (Zakaria *et al.,* 2006; Fong & Paul, 2011). Additionally, the reef crest is associated with higher light irradiance and water movement that can benefit all HFO, since all groups have photosynthetic species and all invertebrate HFO are suspension feeders (Rützler, 1990; Lewis, 2006; Fabricius & De'ath, 2008; Fong & Paul 2011; Rabelo, Rocha & Colares, 2014). However, octocorals are well known colonizers of turbulent environments due to their flexibility (Sánchez, Diaz & Zea, 1997), and their branching morphologies can give them advantage to overshadow other HFO and feed on plankton under high water flows (Labarbera, 1984; Sebens, 1984; McFadden, 1986; Sebens & Johnson, 1991; Fabricius, Genin & Benayahu, 1995), which could explain their higher abundances at the reef crest. Madagascar reef receives waters from an upwelling in the eastern corner of the Yucatan Peninsula (Merino, 1997; Zavala-Hidalgo, 2006) which supplies the nutrients to support high abundances of plankton in the region (Ghinaglia, Herrera-Silveira & Comin, 2004). High levels of nutrients can affect coral health (Vega *et al*., 2014) and species diversity (Duprey, Yasuhara & Baker 2016)~~, while benefiting~~ other HFO (De'Ath & Fabricius, 2010)~~, and leading to~~ sessile communities with low scleractinian coral cover (Arias-Gonzalez *et al.,* 2017)~~, such as~~ Madagascar reef.

~~The places with highest levels of~~ HFO richness provide habitat heterogeneity that could benefit many mobile species. Since each of the HFO provides unique habitats where different species find refuge and food, these regions can be important centers of biodiversity in the ecosystem (Santavy *et al*., 2013). For instance, the lobster *Panulirus argus* (Marx & Herrnkind, 1985;

Herrnkind *et al.,* 1997) and the grouper *Epinephelus striatus* (Dahlgren & Eggleston, 2000) take refuge ~~on~~ sponges, octocorals and macroalgae during their juvenile stage ~~and many~~ species of invertebrates (*e.g.* amphipods, copepods, mollusks, echinoderms and polychaetes) and fish inhabit the micho-habitats of macroalgae (Dulvy *et al*., 2002), octocorals (Goh, Ng & Chou, 1999), sponges (Duffy, 1992; Wulff, 2006), zoanthids (Pérez, Vila-Nova & Santos, 2005) and millepores (Lewis, 2006). Furthermore, HFO serve as food resources; Hawksbill turtles feed on sponges and macroalgae (Bjorndal, 1990) and several species of fish feed on zoanthids (Francini-filho & Moura 2010), macroalgae (Choat, Clements & Robbins, 2002) and sponges (Pawlik *et al.,* 1995), while species of molluscs, echinoderms and crustaceans consume sponges as well (Wulff, 2006).

CONCLUSION

~~The generation of spatial information about~~ the distribution and abundance of biological organisms ~~is~~ needed to establish monitoring programs, detect changes in the community over time and allow conservation planning for the natural ecosystems. The comparison between IDW and OK, a popular but more complex and time consuming methodology, ~~showed that in this case simple was best~~. The only published past studies using IDW in coral reef sessile organisms found this method as a good interpolator for coral cover (Walker *et al.,* 2012; D'Antonio *et al.,* 2016); our results ~~agree with them~~ and we extend ~~its~~ applicability to other important sessile organisms that are ~~emerging under~~ climate change (Norström *et al.,* 2009). We showed that the benthic community of Madagascar reef ~~had important abundances of all the main~~ HFO at the reef crest region, with specific areas ~~having high HFO richness~~. The accurate spatial interpolations created using IDW allowed us to see the spatial variability of each HFO at a biological and spatial resolution that remote sensing would not have been able to produce. This study sets the basis for further biological research projects and conservation management in Madagascar reef and ~~encourages~~ similar studies ~~in the region and other parts of the world~~ where remote sensing technologies are not suitable for use.

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