THE RECENT EXPANSION OF INVASIVE *TUBASTRAEA COCCINEA* THROUGHOUT THE NORTHERN GULF OF MEXICO

An Undergraduate Research Scholars Thesis

by

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ABSTRACT

The Recent Expansion of Invasive *Tubastraea coccinea* Throughout the Gulf of Mexico and its Relation to Oil and Gas Platforms

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Invasive species have large economic and ecological impacts, including agriculture losses, native species replacement, ecological function modification, and altered community structure. Despite this, invasive marine species are relatively understudied. The orange cup coral, *Tubastraea coccinea*, is the first Scleractinia to invade the Western Atlantic. The coral is shown to have negative effects on native reef corals and has been spreading to natural reefs within the Gulf of Mexico (GoM). Our objective is to document the recent range expansion of *T. coccinea* throughout the GoM and produce a species distribution model to project its potential range of invasion and identify the factors for its distribution. Our results show that potential habitat for *T. coccinea* to be mainly distributed within the western half, with the highest probabilities ($0.8 < P$ 1.0) clustered along the Texas and Louisiana borders. Considering the threat that *T. coccinea* presents to native reefs within the GoM, it is important to be able to track and predict its distribution, as well as identify potential factors facilitating its invasion.

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CHAPTER I

INTRODUCTION

Invasive species have large economic and ecological impacts, estimated to cost a minimum of hundreds of billions of dollars globally and may even reach costs of more than one trillion dollars (Pimental et al., 2001). This estimate does not include the negative impacts invasive species have on biodiversity and ecosystem services. Invasive species are known to displace native species, (IUCN, 2000) modify the function and structure of ecosystem communities (Williamson, 1996; Lockwood et al., 2007) and are the second leading cause of native species extinction worldwide (IUCN, 2000).

Invasive marine species negatively impact ecosystem services, such as food provision, ocean nourishment, recreation and tourism, and life cycle maintenance (Katsanevakis et al., 2014). The economic value of ecosystem functions and services globally was estimated to be at least an average of $33 trillion per year (Costanza et al., 1997), and oceans are estimated to provide 63% of that economic value (Costanza et al., 1997; Martinez et al., 2007). Impacts of marine invasive species can lead to substantial economic losses (Perrings, 2002; Wallentinus and Nyberg, 2007; Molnar et al., 2008). Despite this, invasive marine species are relatively understudied when compared to invasive terrestrial species (Rilov and Crooks, 2009).

Orange cup coral (*Tubastraea coccinea*), an invasive marine species, is recorded as the first Scleractinia to invade the Western Atlantic, having been transported to the Caribbean on a ship hull sometime in the late 1930's to early 1940's and has since spread to the Gulf of Mexico (GoM) and Brazil (Cairns, 2000; Figueira de Paula and Creed 2004; Fenner, 2001). Within the GoM, initial sightings were mainly on artificial substrate, such as ship hulls and oil/gas platforms

(Fenner, 2001; Fenner and Banks, 2004; Sammarco et al., 2004). Unfortunately, *T. coccinea* has since been reported in the GoM on natural reef ledges and one colony has been reported growing on a living barrel sponge (Fenner and Banks, 2004; Skinner, 2018). This coral has already been observed encroaching on mussel beds in Brazil's Ilha Grande Bay, demonstrating a real threat to mussel fisheries wherever *T. coccinea* can reach. (Mantelatto and Creed, 2015).

T. coccinea has been shown to inhibit feeding of herbivorous fish, as well as kill and displace native species, therefore disrupting trophic levels within the marine ecosystem (Miranda et. al., 2018; Creed, 2006; Mantelatto and Creed, 2015). The invasion of *T. coccinea* has been observed to cause a decrease in feeding rates of invertebrate-feeding fishes (Miranda et. al., 2018). In Brazil it was noted that the invasive coral had negative effects on the native coral, *Mussismilia hispida*; every specimen that came within 5 cm or less of it showed signs of necrosis, but *T. coccinea* never suffered this condition itself (Creed, 2006). According to Creed (2006) the dead areas were occasionally overgrown by *T. coccinea* as well, indicating its invasive ability.

A likely mode of dispersal for *T. coccinea* is through biofouling on mobile oil/gas platforms (Creed et al., 2017; Seebens et al. 2013; Williams et al. 2013). This is reinforced by characteristics such as *Tubastraea's* delicate larvae. This genus has a relatively slow range expansion, and the larvae generally settle near parental colonies (Creed et al., 2017). Having delicate larvae makes ballast water an unlikely vector because the expulsion of the water could kill them and the larvae settling near the parent colonies would mean they would more likely be growing in the ballast hold of these ships. Another suggested mode of dispersal for *T. coccinea* is regionally by ocean currents, since its larvae can survive for up to 100 days in lab conditions, but where substrate exists, they generally settle and metamorphose in one to three days. Floating debris may also be a possible vector in distributing the coral along the current (Fenner, 2001; Mizrahi et al., 2014). *T. coccinea* can release larva as early as 18 months of age and from as few as two polyps, with multiple reproductive cycles per year (Fenner and Banks, 2004; De Paula et al., 2014).

Fortunately, *T. coccinea* is relatively more accessible for eradication in terms of depth. The coral is found to be limited to depths of 78 meters or less within the GoM, a relatively shallow range when compared to its sister species, *Tubastraea micranthus* (Sammarco et al., 2013). This limitation in range is unlikely to be light related since *T. coccinea* is azooxanthellate and lacks a symbiotic relationship with photosynthetic algae. While eradicating *T. coccinea* by covering the corals in plastic has been successful with isolated groups, focusing on the vector of dispersal rather than the invasive itself may be more effective (Mantelatto and Creed, 2015; Sammarco et al., 2013).

Considering the threat this coral species presents to native ecosystems, its ability to spread regionally, and its continuing spread onto natural reefs throughout the GoM, it is important to be able to track and predict its distribution, as well as identify potential factors facilitating its invasion. Therefore, our objectives are 1) to document the recent range expansion of the invasive *Tubastraea coccinea* throughout the northern Gulf of Mexico and 2) to develop a species distribution model.

CHAPTER II

METHODS

Focal Species

The orange cup coral, *Tubastraea coccinea*, originated from the Indo-Pacific reefs, where it was first described in 1829 near Bora Bora Island in (Creed et al., 2006). It is an azooxanthellate coral, meaning it lacks symbiotic, photosynthetic algae. It is a Scleractinia, or stony coral, that grows in colonies made up of a spongy calcareous base with protruding calcareous cups (Figueira de Paula and Creed, 2004). These protrusions are known as corallites and contain a single polyp each. These cylindrical calcareous protrusions can be up to 11 mm in diameter and can extend up to 4 cm above the spongy base (Cairns, 2000). The colony arrangements of this coral can vary greatly, but it is easily identifiable, with a red to orange body and tentacles that are orange to yellow (Fofonoff et al., 2018), which makes it easily identified as it spreads, allowing for a faster response

Study Area

The GoM has a geographic size of 1.5 million km^2 and as of 2009 has a total 15,419 reported species across 40 phyla (Felder and Camp, 2009). These numbers are estimated to only account for around 80 to 85% of known eukaryotic taxa with the GoM. Our research area is the northern portion of the GoM where it is bounded by five states, including Texas, Louisiana, Mississippi, Alabama and Florida, as seen in Figure 1. The National Oceanic and Atmospheric Administration (NOAA) reports that the Gross Domestic Product resulting from employment in 2015 was $125 billion for the GoM alone (NOAA, 2018). Of the employment accounted for in the GoM, 55% was in Tourism and recreation with the second largest being offshore mineral extraction at 21% (NOAA, 2018). When taking ecosystem goods and services into account, the five states bordering the GoM generate over $2 trillion per year in GDP (Shepard et al., 2013). These estimates do not account for the additional economic value of nonmarket regulating, cultural and supporting services.

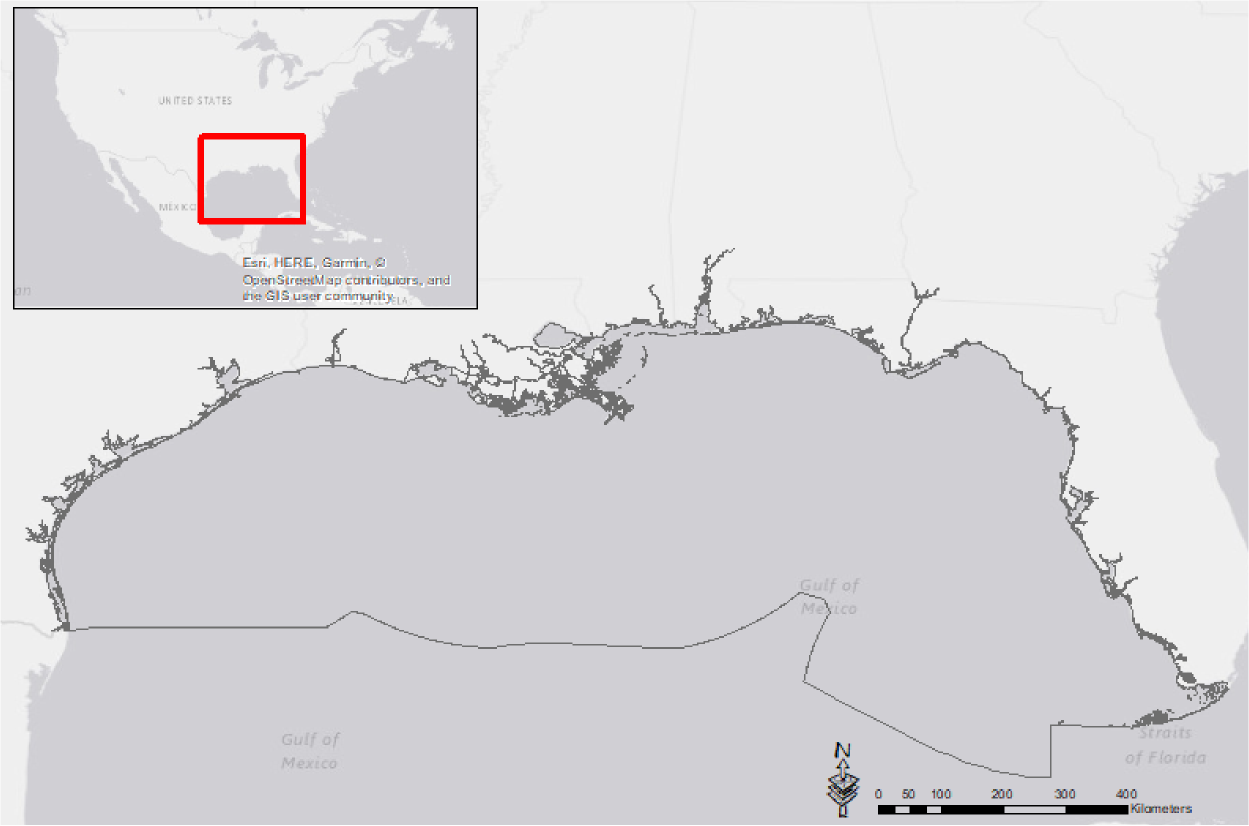

Figure 1. Study area includes the northern portion of the GoM, generated in ArcMap 10.6.1. This region constitutes the United States' exclusive economic zone of the GoM.

Data Collection

For our study area, we used a marine region shapefile of the U.S. portion of the GoM. This was downloaded from marineregions.org, a website operated by the Flanders Marine Institute (2018). The shapefile was produced by the Flanders Marine Institute by combining the exclusive economic zone of the United States within the GoM with the International Hydrographic Organization sea area. We obtained occurrence records to map the distribution of

T. coccinea from the scientific database, Web of Science, as well as from Global Biodiversity Information Facility (GBIF) and Ocean Biogeographic Information System (OBIS). GBIF is an international research infrastructure coordinated by the Secretariat in Copenhagen. OBIS is coordinated by the United States Geological Survey, a scientific agency of the United States. From these records, we were particularly interested in collecting coordinates and site type (e.g. natural reef, artificial reef or oil/gas platform). We selected 42 variables that have been suggested in the literature to have physiological and ecological relevance for marine organisms, including various benthic and surface variables (Tyberghein et al., 2012; Assis et al. 2017) (Appendix 1). The environmental variables were downloaded from Bio-Oracle (www.bio-oracle.org), which provides uniform, high-resolution marine data layers for ecological modelling. A flow chart of our entire process is provided in Figure 2.

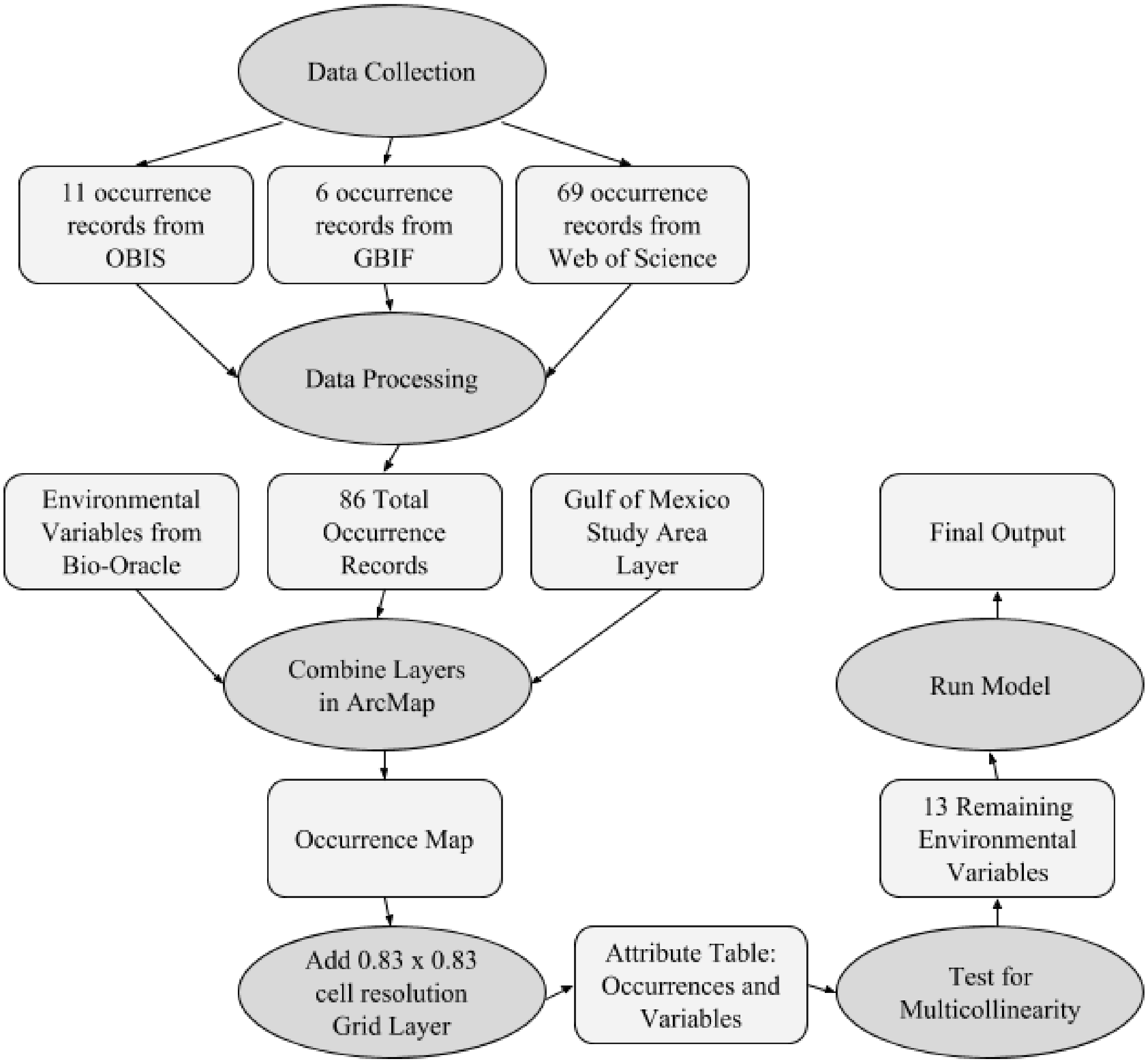

Figure 2. A flow chart showing our processing methods beginning with data collection.

Data Analysis

We overlaid the processed occurrence data and study area over the light gray canvas basemap to produce the occurrence map in Figure 3. To add the environmental variables, each of the variables were downloaded as TIFF raster files from Bio-ORACLE and combined with our occurrence map in ArcMap 10.6.1 (ESRI, 2011). Next, we overlaid a geo-referenced grid containing 0.083 degree × 0.083 degree cells with the combined occurrence map and variable layers in order to derive a value for each of the 42 potential predictor variables at the centroids within each cell using bilinear interpolation. We used Pearson's correlation coefficient to measure independence among the 42 variables and eliminated 29 variables with high correlation (Pearson's correlation coefficient either ≥ 0.80 or ≤ -0.80, Appendix 2), thus retaining 13 variables for further analysis (Table 1). We also randomly generated the same number of pseudo-absences as available presences of *T. coccinea* (Barbet-Massin et al., 2012). We then merged the explanatory variable data associated with *T. coccinea* (69 points) and pseudo-absences (69 points) into polygons representing 9,720 0.083 degree × 0.083 degree cells.

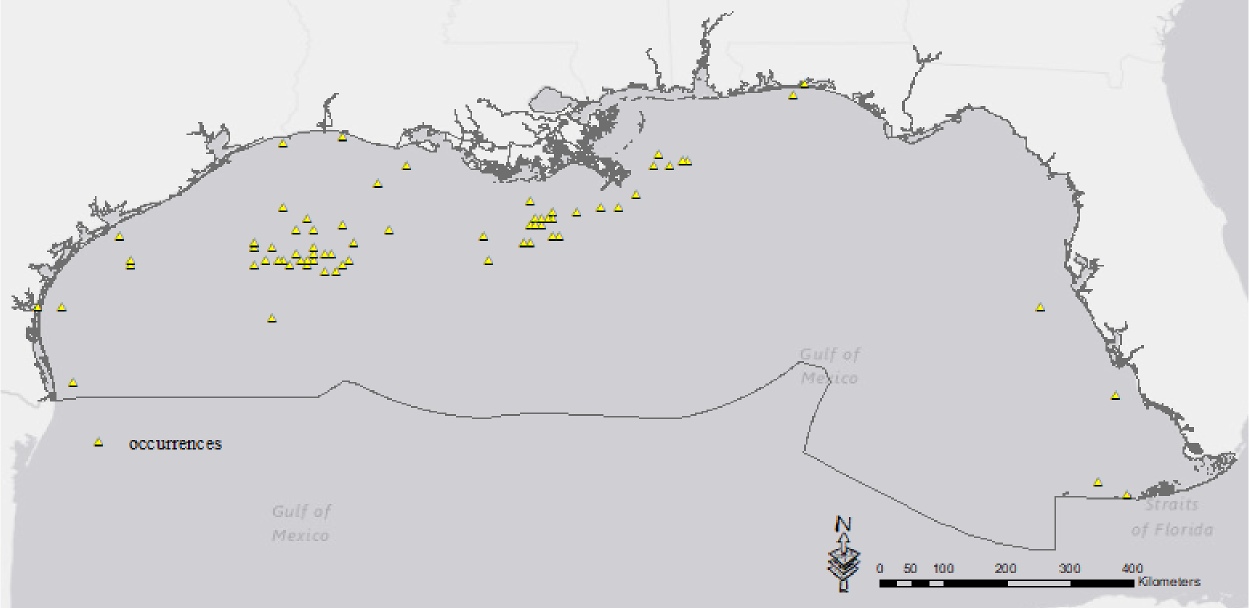

Figure 3. Occurrence map showing occurrence points as yellow triangles with the study area.

Table 1. Abbreviations, descriptions and descriptive statistics for the benthic and surface variables included in the final model.

Variable	**Description**	**Mean**	**Minimum**	**Maximum**
Benthic variables				
chla.max.b	maximum chlorophyll (mg.m-3)	0.38818	0.00449	3.38342
chla.min.b	minimum chlorophyll (mg.m-3)	0.02992	0.00435	0.38446
curr.v.max.b	maximum current velocity (m-1)	0.12334	0.00578	1.00550
curr.v.min.b	minimum current velocity (m-1)	0.11374	0.01082	0.69053
o2.max.b	maximum dissolved oxygen (mol.m-3)	216.31491	145.20961	312.96687
o2.min.b	minimum dissolved oxygen (mol.m-3)	185.25509	120.18250	210.60578
light.max.b	maximum light bottom	0.53822	0	31.61150
light.min.b	minimum light bottom	1.96473	0	21.03824
salinity.max.b	maximum salinity (PSS)	35.50325	30.81167	36.78182
salinity.min.b	minimum salinity (PSS)	34.27485	13.40136	36.32946
silicate.min.b	minimum silicate (mol.m-3)	14.43593	3.03650	33.50874
Surface variables				
cloud.mean.s	mean cloud cover (%)	-1.22420	-2.56096	-0.35865
diff.att.min.s	minimum diffuse attenuation (m-1)	1.00583	-0.41653	14.37526

We conducted our analysis using boosted regression trees (Elith et al., 2008). For boosted regression trees, the probability (*P*) of *T. coccinea* presence (*y* = 1) at a location with the vector of potential explanatory variables (***X***) is given by *P*(y = 1|***X***) and is modelled via the logit: logit *P*(*y* = 1|***X***) = *f*(***X***). We fitted our model in R 3.4.4 (R Core Team, 2013) using the gbm package version 1.5-7 (Ridgeway 2006). The optimal model was determined by altering the learning rate and tree complexity (the number of split nodes in a tree) until the predictive deviance was minimized without over-fitting, and by limiting our choice of the final model to those that contained at least 1000 trees (where each successive tree is built for the prediction residuals of the preceding tree) (Elith et al. 2008). Once the optimal combination of learning rate and tree complexity was found, model performance was evaluated using a ten-fold cross-validation procedure with resubstitution. For each cross-validation trial, 60% of the dataset was randomly selected for model fitting and the excluded 40% was used for testing. We calculated the response variance explained, the area under the receiver operator characteristic curve (AUC), the overall accuracy, the omission error rate, and the commission error rate based on the aggregated CV results. We evaluated the reliability and validity of our models as fair ($0.50 < AUC \leq 0.75$), good ($0.75 < AUC \leq 0.92$), very good ($0.92 < AUC \leq 0.97$), or excellent ($0.97 < AUC \leq 1.00$) based on the value of AUC (Hosmer and Lemeshow, 2000). We then used the gbm library to derive the relative influence of each potential explanatory variable in the model and constructed partial dependence plots for the most influential variables. Finally, we used this optimal model to calculate probability of *T. coccinea* presence in each cell for 10 times and averaged them. We overlaid these mean probabilities of presence on a map of the study area using ArcMap 10.6.1 (ESRI 2011).

CHAPTER III

RESULTS

Thirteen variables were included in the final model, with variables associated with benthic and surface variables for approximately 81.72% and 18.28%, respectively, of the contribution in the overall model (Fig. 4). Examination of the relative contribution of the predictor variables indicated that the top six accounted for approximately 74.40% of the contribution in the overall model. Of the six most influential model variables, four were benthic and two were surface variables. Maximum current velocity, minimum silicate, maximum salinity, and minimum chlorophyll were the first, second, fourth, and fifth most influential variables, contributing 29.48%, 12.31%, 8.09%, and 7.38%, respectively. Minimum diffuse attenuation and mean cloud cover were the third and sixth most important variable contributing 10.25% and 7.20%, respectively.

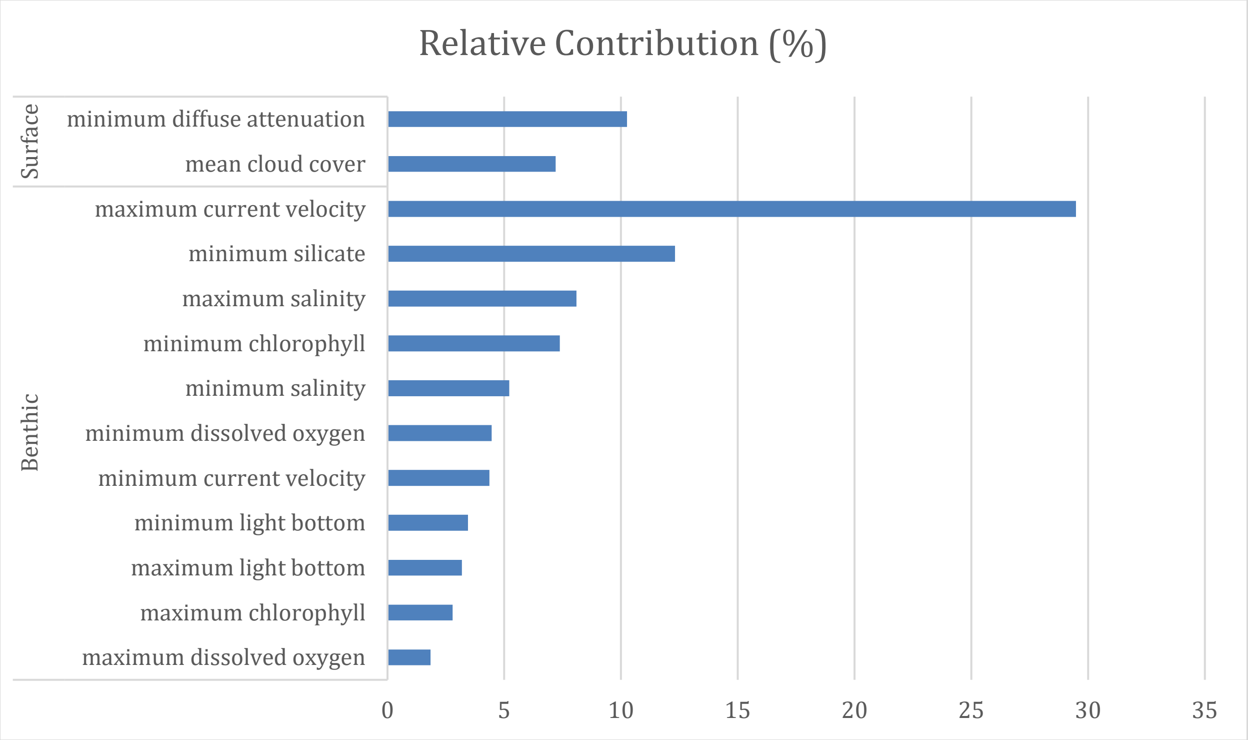

Figure 4. Relative contributions (%) of the 13 environmental variables used in our final model.

Partial dependence plots indicated that *T. coccinea* occurrences were associated with surface conditions characterized by minimum diffuse attenuation between 0.5 m-1 and 11 m-1 (Fig. 5c) and mean cloud cover between -2.4% and -1.65% as well as -1.2% and -0.95% (Fig. 5f). Occurrences also were associated with benthic conditions characterized by (1) maximum current velocity between 0.17 m-1 and 1.0 m-1 (Fig. 5a), (2) minimum silicate between 4 mol m-3 and 5 mol m-3 (Fig. 5b), (3) maximum salinity between 35.6 PSS and 36.9 PSS (Fig. 5d), (4) minimum chlorophyll between 0.025 mg m-3 and 0.10 mg m-3 (Fig. 5e), (5) minimum salinity between 35.1 PSS and 36 PSS (Fig. 5g), (6) minimum dissolved oxygen between 203 mol m-3 and 215 mol m-3 (Fig. 5h), (7) minimum current velocity between 0.11 m-1 and 0.20 m-1 (Fig. 5i), (8) minimum light bottom between 0.0 and 4.0 (Fig. 5j), (9) maximum light bottom between 0.0 and 0.1 (Fig. 5k), (10) maximum chlorophyll between 0.0 mg m-3 and 0.48 mg m-3 (Fig. 5l) and (11) maximum dissolved oxygen between 232 mol m-3 and 282 mol m-3 (Fig. 5m).

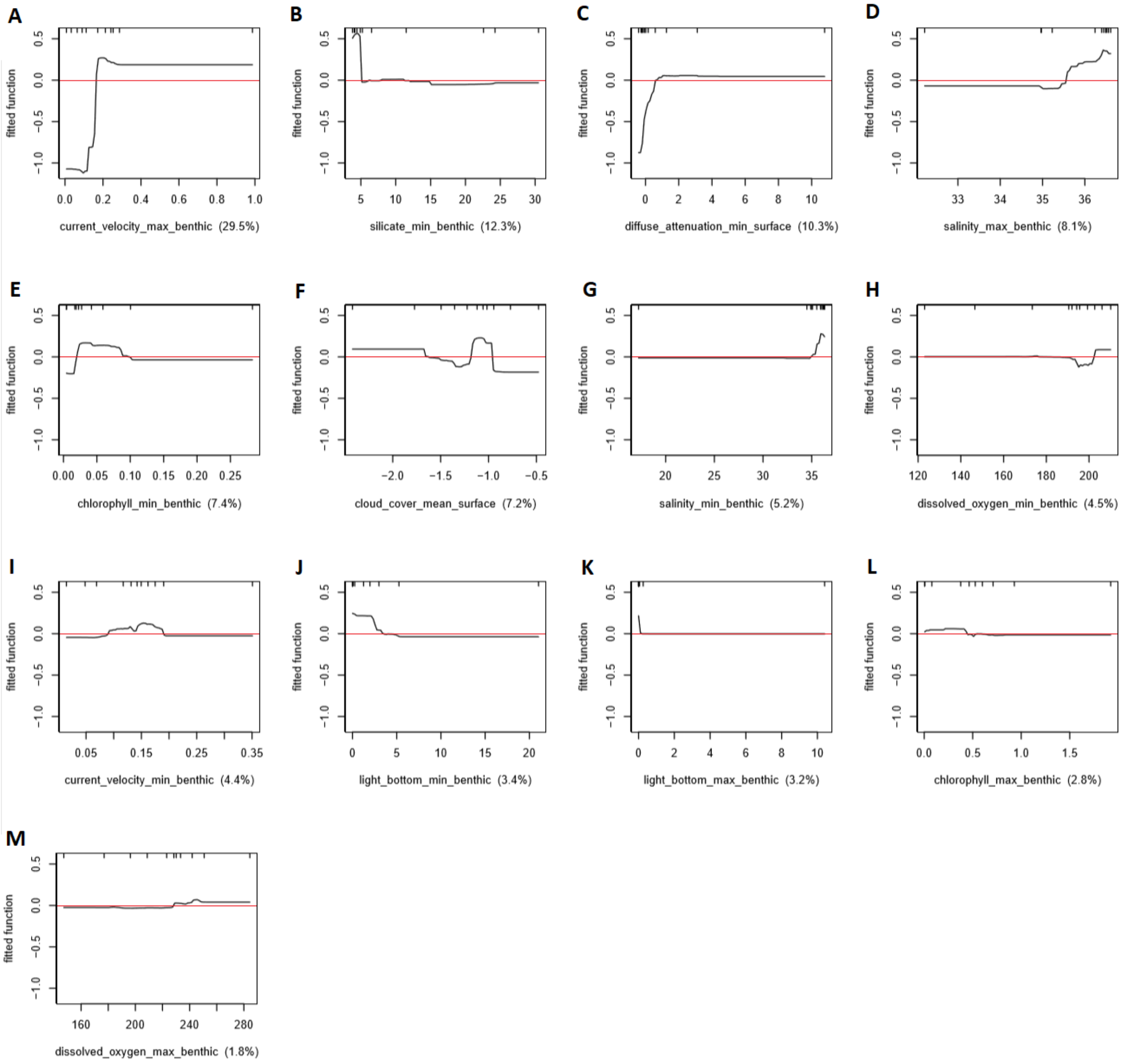

Figure 5. Partial dependence plots for the 13 variables included in the final model. The y-axis represents the logit scale used for the indicated variable, hashmarks at the top of the plot indicate the locations of the sample sites along the range of the variables.

Our analyses suggest that potential habitat for *T. coccinea* in the northern GoM, considering its association with the surface and benthic variables mentioned in the previous paragraph, is most likely to be in the western half, with the highest probabilities (0.8 < P 1.0) mainly along the Texas and Louisiana borders (Fig. 6). Approximately 73, 8, 7, 5, 6, and 0.2%

of the cells fell within the $P \leq 0.5$, $0.5 < P \leq 0.6$, $0.6 < P \leq 0.7$, $0.7 < P \leq 0.8$, $0.8 < P \leq 0.9$, and $0.9 < P \leq 1.0$ estimated probability of occurrence (P) categories, respectively.

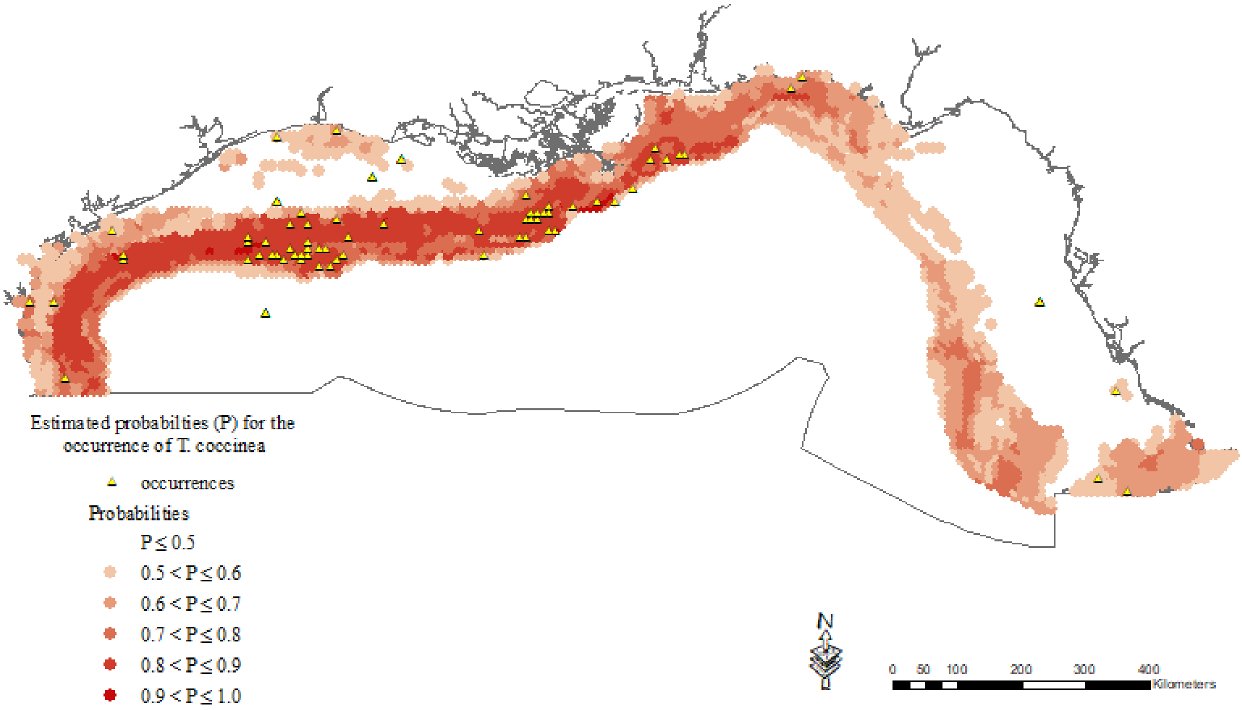

Figure 6. Estimated probabilities of occurrence of *T. coccinea* in the northern Gulf of Mexico.

CHAPTER IV

DISCUSSION

Although *T. coccinea* may be easier to eradicate thanks to its depth distribution, once invasive species have been established, resources are generally better allocated toward mitigation and containment (Park, 2004). One technique is to focus on the vectors of invasion. It is becoming increasingly apparent that biofouling of oil and gas platforms act as a vector for *T. coccinea* to spread (Hickerson et al., 2008). The northern part of the GoM is one of the most active locations of oil and gas exploration worldwide, accounting for 25% of oil and 14% of natural gas production offshore in U.S. waters (Hickerson et al., 2008). There are at least 14 production platforms and about 184.31 km of pipeline in within the Eastern and Western Flower Garden Bank zones (Hickerson et al., 2008). As for decommissioned platforms, there are at least 15 near the Flower Garden Bank National Marine Sanctuary, bringing the total to at least 29 platforms that could be used as stepping stones for invasive corals (Hickerson et al., 2008).

T. coccinea has been found flourishing on a gas platform named High Island A389A (HIA389A), which resides within the boundaries of the East Flower Garden Bank, only 2 km away from protected corals (Hickerson et al., 2008). Subsequent surveys uncovered colonies of *T. coccinea* had already taken root on the Eastern Flower Garden Bank and 52 km east-southeast at Geyer Bank (Hickerson et al., 2008). Later, another 100+ colonies were reported at Geyer Bank and several more at Sonnier Bank (Hickerson et al., 2008). Current technology to prevent biofouling, such as sacrificial zinc anodes and induced cathodic currents may be obsolete at repelling *T. coccinea.* Large, dense groups of *T. coccina* have been reported on platforms growing directly on the anodes (Sammarco et al., 2004).

Considering the threat this coral species presents to native reefs, its ability to spread regionally, and its continuing spread onto natural reefs throughout the Gulf of Mexico, it is important to be able to track and predict its distribution, as well as identify potential vectors facilitating its invasion. It is our hope that our model will help predict where it is likely to colonize and help future placement of potential vectors within the GoM, such as artificial substrate that may act as stepping stones to natural reefs. This species distribution model will allow for planning to be carried out before sites for artificial reefs are designated. To effectively incorporate this model into future management, it is best to link this research with key spatial data that would help identify potential sources of introduction, vectors to existing reefs or platforms in hopes of reducing future invasive species introduction and further distribution.

CHAPTER V

CONCLUSION

Surface and benthic variables can be used to predict the distribution of the invasive marine species, *T. coccinea,* which has expanded its range throughout the Western Atlantic. Of the variables used in the final model, salinity is considered one of the most important factors influencing marine ecosystems (Tyberghein et al., 2012; Assis et al. 2017). Chlorophyll is an indicator of primary productivity, while cloud cover is considered an indirect proxy for incoming light or UV radiation. *T. coccinea's* predicted distribution is widely disbursed, although the highest probability is mainly in the western portion. The sites where *T. coccinea* has been reported is clustered around two areas, one off the coast of Texas and the other along Louisiana. These clusters may reflect areas that are heavily sampled as opposed to limitations to where *T. coccinea* exists. Because marine ecosystems lack complete sampling coverage, species distribution models are necessary to inform policy makers and conservation management.

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APPENDIX

Supplementary Material 1

Abbreviations, descriptions and descriptive statistics for the surface and benthic variables identified as potential factors influencing the possible distribution of *Tubastraea coccinea* throughout the northern Gulf of Mexico.

Surface
cloud.max.s: maximum cloud cover (%)
cloud.mean.s: mean cloud cover (%)
cloud.min.s: minimum cloud cover (%)
diff.att.max.s: maximum diffuse attenuation (m-1)
diff.att.mean.s: mean diffuse attenuation (m-1)
diff.att.min.s: minimum diffuse attenuation (m-1)

Benthic
chla.max.b: maximum chlorophyll (mg.m-3)
chla.mean.b: mean chlorophyll (mg.m-3)
chla.min.b: minimum chlorophyll (mg.m-3)
curr.v.max.b: maximum current velocity (m-1)
curr.v.mean.b: mean current velocity (m-1)
curr.v.min.b: minimum current velocity (m-1)
O2.max.b: maximum dissolved oxygen (mol.m-3)
light.mean.b: mean light bottom
light.min.b: minimum light bottom
nitrate.max.b: maximum nitrate (mol.m-3)
nitrate.mean.b: mean nitrate (mol.m-3)
nitrate.min.b: minimum nitrate (mol.m-3)
phos.max.b: maximum phosphate (mol.m-3)
phos.mean.b: mean phosphate (mol.m-3)
phos.min.b: minimum phosphate (mol.m-3)
plankton.max.b: maximum phytoplankton (umol.m-3)
plankton.mean.b: mean phytoplankton (umol.m-3)
plankton.min.b: minimum phytoplankton (umol.m-3)
pp.max.b: maximum primary productivity (g.m-3.day-1)
pp.mean.b: mean primary productivity (g.m-3.day-1)
pp.min.b: minimum primary productivity (g.m-3.day-1)
salinity.max.b: maximum salinity (PSS)
salinity.mean.b: mean salinity (PSS)
salinity.min.b: minimum salinity (PSS)

silicate.max.b: maximum silicate (mol.m-3)
silicate.mean.b: mean silicate (mol.m-3)
silicate.min.b: minimum silicate (mol.m-3)
temp.max.b: maximum temperature (ºC)
temp.mean.b: mean temperature (ºC)
temp.min.b: minimum temperature (ºC)
O2.mean.b: mean dissolved oxygen (mol.m-3)
O2.min.b: minimum dissolved oxygen (mol.m-3)
iron.max.b: maximum iron (umol.m-3)
iron.mean.b: mean iron (umol.m-3)
iron.min.b: minimum iron (umol.m-3)
light.max.b: maximum light bottom

Supplementary Material 2

Correlation Matrix containing all twenty environmental layers. Positive correlation $\geq$.80 or negative correlation $\leq$-0.60 shown in red. For variable names refer to Supplementary material 1.

	cloud.max.s	cloud.mean.s	cloud.min.s	diff.att.max.s	diff.att.mean.s	diff.att.min.s
cloud.max.s	1.000					
cloud.mean.s	0.912	1.000				
cloud.min.s	0.839	0.938	1.000			
diff.att.max.s	-0.590	-0.676	-0.642	1.000		
diff.att.mean.s	-0.588	-0.667	-0.634	0.993	1.000	
diff.att.min.s	-0.569	-0.641	-0.605	0.971	0.991	1.000
chla.max.b	-0.534	-0.635	-0.615	0.519	0.517	0.497
chla.mean.b	-0.444	-0.508	-0.498	0.582	0.587	0.583
chla.min.b	-0.367	-0.412	-0.404	0.565	0.573	0.579
curr.v.max.b	-0.206	-0.226	-0.293	0.082	0.070	0.049
curr.v.mean.b	-0.297	-0.304	-0.348	0.148	0.146	0.142
curr.v.min.b	-0.234	-0.279	-0.362	0.213	0.198	0.168
O2.max.b	-0.621	-0.682	-0.670	0.677	0.680	0.652
light.mean.b	-0.586	-0.648	-0.638	0.603	0.617	0.630
light.min.b	-0.701	-0.786	-0.769	0.639	0.640	0.625
nitrate.max.b	0.415	0.515	0.572	-0.176	-0.152	-0.097
nitrate.mean.b	0.529	0.646	0.692	-0.344	-0.322	-0.268
nitrate.min.b	0.593	0.717	0.754	-0.464	-0.446	-0.397
phos.max.b	0.673	0.792	0.816	-0.607	-0.594	-0.547
phos.mean.b	0.651	0.773	0.800	-0.579	-0.565	-0.519
phos.min.b	0.632	0.757	0.787	-0.559	-0.545	-0.500

plankton.max.b	-0.611	-0.707	-0.674	0.651	0.655	0.641
plankton.mean.b	-0.549	-0.619	-0.599	0.712	0.719	0.713
plankton.min.b	-0.592	-0.664	-0.653	0.761	0.768	0.759
pp.max.b	-0.567	-0.666	-0.641	0.599	0.598	0.580
pp.mean.b	-0.424	-0.472	-0.442	0.634	0.645	0.652
pp.min.b	-0.303	-0.329	-0.290	0.560	0.574	0.592
salinity.max.b	-0.052	-0.091	-0.154	-0.321	-0.345	-0.389
salinity.mean.b	0.229	0.252	0.206	-0.639	-0.659	-0.685
salinity.min.b	0.311	0.350	0.315	-0.714	-0.731	-0.747
silicate.max.b	0.232	0.346	0.426	-0.007	0.022	0.069
silicate.mean.b	0.369	0.502	0.563	-0.178	-0.151	-0.100
silicate.min.b	0.477	0.616	0.661	-0.333	-0.310	-0.261
temp.max.b	-0.685	-0.811	-0.837	0.617	0.604	0.558
temp.mean.b	-0.659	-0.788	-0.820	0.577	0.561	0.515
temp.min.b	-0.557	-0.688	-0.735	0.433	0.413	0.365
O2.mean.b	-0.473	-0.515	-0.502	0.494	0.494	0.467
O2.min.b	-0.273	-0.279	-0.261	0.292	0.292	0.272
iron.max.b	-0.632	-0.705	-0.671	0.822	0.828	0.822
iron.mean.b	-0.624	-0.686	-0.650	0.828	0.839	0.838
iron.min.b	-0.579	-0.616	-0.585	0.828	0.844	0.849
light.max.b	-0.318	-0.357	-0.359	0.508	0.533	0.559

	chla.max.b	chla.mean.b	chla.min.b	curr.v.max.b	curr.v.mean.b	curr.v.min.b
cloud.max.s						
cloud.mean.s						
cloud.min.s						
diff.att.max.s						
diff.att.mean.s						
diff.att.min.s						
chla.max.b	1.000					
chla.mean.b	0.862	1.000				
chla.min.b	0.679	0.936	1.000			
curr.v.max.b	0.256	0.240	0.216	1.000		
curr.v.mean.b	0.131	0.126	0.124	0.886	1.000	
curr.v.min.b	0.365	0.346	0.311	0.779	0.604	1.000
O2.max.b	0.740	0.645	0.521	0.136	0.163	0.302
light.mean.b	0.365	0.307	0.297	0.206	0.356	0.199
light.min.b	0.439	0.316	0.271	0.272	0.416	0.269
nitrate.max.b	-0.448	-0.211	-0.043	-0.531	-0.400	-0.562
nitrate.mean.b	-0.577	-0.367	-0.210	-0.540	-0.407	-0.606
nitrate.min.b	-0.670	-0.505	-0.364	-0.526	-0.390	-0.623

phos.max.b	-0.767	-0.617	-0.472	-0.447	-0.360	-0.549
phos.mean.b	-0.764	-0.625	-0.485	-0.477	-0.367	-0.583
phos.min.b	-0.748	-0.624	-0.494	-0.497	-0.370	-0.608
plankton.max.b	0.973	0.881	0.738	0.194	0.125	0.315
plankton.mean.b	0.868	0.966	0.903	0.182	0.130	0.303
plankton.min.b	0.830	0.937	0.900	0.224	0.183	0.346
pp.max.b	0.976	0.890	0.735	0.198	0.119	0.311
pp.mean.b	0.775	0.940	0.912	0.069	0.036	0.180
pp.min.b	0.581	0.819	0.881	-0.025	-0.024	0.051
salinity.max.b	0.010	-0.186	-0.295	0.415	0.268	0.384
salinity.mean.b	-0.358	-0.547	-0.621	0.190	0.112	0.091
salinity.min.b	-0.464	-0.644	-0.701	0.108	0.062	-0.014
silicate.max.b	-0.257	-0.098	0.005	-0.570	-0.380	-0.577
silicate.mean.b	-0.424	-0.260	-0.146	-0.606	-0.410	-0.645
silicate.min.b	-0.552	-0.405	-0.290	-0.590	-0.398	-0.664
temp.max.b	0.749	0.613	0.482	0.464	0.366	0.579
temp.mean.b	0.730	0.600	0.473	0.513	0.399	0.607
temp.min.b	0.668	0.554	0.436	0.619	0.456	0.661
O2.mean.b	0.698	0.565	0.408	0.113	0.139	0.219
O2.min.b	0.492	0.355	0.205	0.008	0.087	0.040
iron.max.b	0.747	0.823	0.800	0.074	0.104	0.217
iron.mean.b	0.696	0.789	0.784	0.020	0.072	0.169
iron.min.b	0.585	0.720	0.740	-0.060	0.026	0.102
light.max.b	0.166	0.205	0.237	0.169	0.275	0.122

	O2.max.b	light.mean.b	light.min.b	nitrate.max.b	nitrate.mean.b	nitrate.min.b
cloud.max.s						
cloud.mean.s						
cloud.min.s						
diff.att.max.s						
diff.att.mean.s						
diff.att.min.s						
chla.max.b						
chla.mean.b						
chla.min.b						
curr.v.max.b						
curr.v.mean.b						
curr.v.min.b						
O2.max.b	1.000					
light.mean.b	0.542	1.000				
light.min.b	0.649	0.917	1.000			

nitrate.max.b	-0.515	-0.322	-0.477	1.000		
nitrate.mean.b	-0.630	-0.414	-0.573	0.974	1.000	
nitrate.min.b	-0.700	-0.465	-0.614	0.911	0.979	1.000
phos.max.b	-0.829	-0.555	-0.700	0.821	0.918	0.965
phos.mean.b	-0.800	-0.527	-0.668	0.836	0.932	0.979
phos.min.b	-0.766	-0.507	-0.643	0.838	0.935	0.985
plankton.max.b	0.791	0.461	0.528	-0.357	-0.515	-0.634
plankton.mean.b	0.739	0.440	0.466	-0.199	-0.373	-0.521
plankton.min.b	0.773	0.507	0.542	-0.256	-0.433	-0.576
pp.max.b	0.767	0.421	0.488	-0.356	-0.502	-0.613
pp.mean.b	0.597	0.340	0.326	0.029	-0.142	-0.300
pp.min.b	0.428	0.298	0.249	0.251	0.085	-0.081
salinity.max.b	0.004	-0.050	0.069	-0.784	-0.663	-0.542
salinity.mean.b	-0.340	-0.305	-0.227	-0.464	-0.279	-0.110
salinity.min.b	-0.450	-0.372	-0.314	-0.326	-0.130	0.046
silicate.max.b	-0.166	-0.153	-0.261	0.888	0.845	0.782
silicate.mean.b	-0.339	-0.274	-0.404	0.918	0.924	0.896
silicate.min.b	-0.475	-0.365	-0.502	0.889	0.941	0.951
temp.max.b	0.764	0.553	0.694	-0.802	-0.910	-0.966
temp.mean.b	0.726	0.536	0.677	-0.828	-0.928	-0.978
temp.min.b	0.594	0.447	0.581	-0.871	-0.944	-0.973
O2.mean.b	0.939	0.420	0.520	-0.482	-0.549	-0.580
O2.min.b	0.763	0.280	0.357	-0.310	-0.325	-0.315
iron.max.b	0.737	0.565	0.598	-0.112	-0.307	-0.465
iron.mean.b	0.722	0.571	0.595	-0.067	-0.259	-0.420
iron.min.b	0.665	0.541	0.541	0.024	-0.160	-0.320
light.max.b	0.305	0.845	0.675	-0.122	-0.191	-0.235

	phos.max.b	phos.mean.b	phos.min.b	plankton.max.b	plankton.mean.b	plankton.min.b
cloud.max.s						
cloud.mean.s						
cloud.min.s						
diff.att.max.s						
diff.att.mean.s						
diff.att.min.s						
chla.max.b						
chla.mean.b						
chla.min.b						
curr.v.max.b						
curr.v.mean.b						
curr.v.min.b						

O2.max.b						
light.mean.b						
light.min.b						
nitrate.max.b						
nitrate.mean.b						
nitrate.min.b						
phos.max.b	1.000					
phos.mean.b	0.996	1.000				
phos.min.b	0.986	0.996	1.000			
plankton.max.b	-0.767	-0.754	-0.734	1.000		
plankton.mean.b	-0.673	-0.663	-0.650	0.929	1.000	
plankton.min.b	-0.723	-0.712	-0.699	0.905	0.984	1.000
pp.max.b	-0.746	-0.733	-0.711	0.988	0.926	0.893
pp.mean.b	-0.471	-0.460	-0.446	0.849	0.966	0.931
pp.min.b	-0.264	-0.249	-0.240	0.688	0.861	0.829
salinity.max.b	-0.359	-0.392	-0.415	-0.126	-0.264	-0.234
salinity.mean.b	0.090	0.062	0.043	-0.505	-0.643	-0.633
salinity.min.b	0.243	0.217	0.201	-0.607	-0.742	-0.740
silicate.max.b	0.626	0.665	0.694	-0.152	-0.037	-0.083
silicate.mean.b	0.772	0.808	0.834	-0.340	-0.222	-0.273
silicate.min.b	0.865	0.895	0.918	-0.496	-0.392	-0.443
temp.max.b	-0.988	-0.990	-0.988	0.755	0.667	0.716
temp.mean.b	-0.982	-0.989	-0.992	0.724	0.640	0.691
temp.min.b	-0.931	-0.952	-0.966	0.623	0.546	0.596
O2.mean.b	-0.713	-0.679	-0.633	0.708	0.632	0.650
O2.min.b	-0.456	-0.412	-0.354	0.487	0.415	0.423
iron.max.b	-0.646	-0.621	-0.602	0.867	0.932	0.940
iron.mean.b	-0.608	-0.579	-0.560	0.831	0.910	0.922
iron.min.b	-0.513	-0.482	-0.463	0.737	0.850	0.864
light.max.b	-0.298	-0.281	-0.270	0.244	0.291	0.352

	pp.max.b	pp.mean.b	pp.min.b	salinity.max.b	salinity.mean.b	salinity.min.b
cloud.max.s						
cloud.mean.s						
cloud.min.s						
diff.att.max.s						
diff.att.mean.s						
diff.att.min.s						
chla.max.b						
chla.mean.b						
chla.min.b						

curr.v.max.b						
curr.v.mean.b						
curr.v.min.b						
O2.max.b						
light.mean.b						
light.min.b						
nitrate.max.b						
nitrate.mean.b						
nitrate.min.b						
phos.max.b						
phos.mean.b						
phos.min.b						
plankton.max.b						
plankton.mean.b						
plankton.min.b						
pp.max.b	1.000					
pp.mean.b	0.860	1.000				
pp.min.b	0.696	0.948	1.000			
salinity.max.b	-0.101	-0.418	-0.554	1.000		
salinity.mean.b	-0.469	-0.722	-0.787	0.876	1.000	
salinity.min.b	-0.572	-0.791	-0.829	0.773	0.981	1.000
silicate.max.b	-0.149	0.153	0.319	-0.828	-0.546	-0.425
silicate.mean.b	-0.331	-0.017	0.170	-0.747	-0.392	-0.254
silicate.min.b	-0.480	-0.185	0.007	-0.629	-0.218	-0.068
temp.max.b	0.728	0.468	0.269	0.368	-0.094	-0.250
temp.mean.b	0.701	0.438	0.239	0.413	-0.048	-0.206
temp.min.b	0.613	0.344	0.147	0.527	0.085	-0.072
O2.mean.b	0.711	0.513	0.340	0.008	-0.249	-0.333
O2.min.b	0.509	0.347	0.219	-0.069	-0.180	-0.218
iron.max.b	0.839	0.898	0.842	-0.393	-0.754	-0.839
iron.mean.b	0.797	0.884	0.848	-0.415	-0.762	-0.844
iron.min.b	0.698	0.843	0.833	-0.462	-0.772	-0.841
light.max.b	0.215	0.241	0.241	-0.132	-0.295	-0.330

	silicate.max.b	silicate.mean.b	silicate.min.b	temp.max.b	temp.mean.b	temp.min.b
cloud.max.s						
cloud.mean.s						
cloud.min.s						
diff.att.max.s						
diff.att.mean.s						
diff.att.min.s						

chla.max.b						
chla.mean.b						
chla.min.b						
curr.v.max.b						
curr.v.mean.b						
curr.v.min.b						
O2.max.b						
light.mean.b						
light.min.b						
nitrate.max.b						
nitrate.mean.b						
nitrate.min.b						
phos.max.b						
phos.mean.b						
phos.min.b						
plankton.max.b						
plankton.mean.b						
plankton.min.b						
pp.max.b						
pp.mean.b						
pp.min.b						
salinity.max.b						
salinity.mean.b						
salinity.min.b						
silicate.max.b	1.000					
silicate.mean.b	0.967	1.000				
silicate.min.b	0.889	0.974	1.000			
temp.max.b	-0.658	-0.804	-0.899	1.000		
temp.mean.b	-0.704	-0.842	-0.925	0.996	1.000	
temp.min.b	-0.807	-0.916	-0.966	0.948	0.972	1.000
O2.mean.b	-0.096	-0.237	-0.339	0.609	0.577	0.470
O2.min.b	0.085	-0.006	-0.067	0.320	0.291	0.203
iron.max.b	0.053	-0.145	-0.331	0.652	0.612	0.472
iron.mean.b	0.096	-0.096	-0.284	0.616	0.571	0.419
iron.min.b	0.167	-0.004	-0.186	0.527	0.476	0.311
light.max.b	-0.022	-0.105	-0.172	0.301	0.293	0.242

	O2.mean.b	O2.min.b	iron.max.b	iron.mean.b	iron.min.b	light.max.b
cloud.max.s						
cloud.mean.s						
cloud.min.s						

diff.att.max.s						
diff.att.mean.s						
diff.att.min.s						
chla.max.b						
chla.mean.b						
chla.min.b						
curr.v.max.b						
curr.v.mean.b						
curr.v.min.b						
O2.max.b						
light.mean.b						
light.min.b						
nitrate.max.b						
nitrate.mean.b						
nitrate.min.b						
phos.max.b						
phos.mean.b						
phos.min.b						
plankton.max.b						
plankton.mean.b						
plankton.min.b						
pp.max.b						
pp.mean.b						
pp.min.b						
salinity.max.b						
salinity.mean.b						
salinity.min.b						
silicate.max.b						
silicate.mean.b						
silicate.min.b						
temp.max.b						
temp.mean.b						
temp.min.b						
O2.mean.b	1.000					
O2.min.b	0.929	1.000				
iron.max.b	0.582	0.366	1.000			
iron.mean.b	0.554	0.340	0.992	1.000		
iron.min.b	0.483	0.282	0.952	0.980	1.000	
light.max.b	0.215	0.140	0.372	0.385	0.386	1.000