CHAPTER 2

MODELING THE DISTRIBUTION AND ECOLOGY OF *TRICHOSOLEN* BLOOMS ON CORAL REEFS WORLDWIDE

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ABSTRACT

Worldwide blooms of the green alga *Trichosolen* have been reported on damaged coral reefs following catastrophic events. However, the global distribution of *Trichosolen* and the factors triggering such blooms remained elusive because of a paucity of occurrence records. This study presents a presence-only niche modeling approach to map the potential distribution and delineate bloom risk areas as well as to identify environmental response optima for non-blooming occurrences and blooms. The modeled suitability map revealed a pantropical to subtropical distribution, while high suitability values delineated bloom risk areas including important tropical reef systems where *Trichosolen* has not yet been reported from. While both blooms and non-bloom occurrences show a strong preference for high temperatures, blooms responded better to broader nutrient ranges than non-blooms.

INTRODUCTION

Coral communities are subject to extensive mechanical damage from both natural and anthropogenic causes, including cyclonic wave action, earthquakes and tsunamis, *Acanthaster* outbreaks, construction, ship groundings and removals, dynamite fishing, boat anchoring, diving and coral removal. The resulting lesions and cleared substrates on coral reef systems are susceptible to quick overgrowth by rapid colonizers such as benthic diatoms, cyanobacteria and turf algae (Rogers et al., 1991; Russ & McCook, 1999; Schroeder et al., 2008; Titlyanov et al., 2008). These rapid colorizations (sometimes involving only one taxonomic entity) either mark the start of a complete phase shift (e.g. Diaz-Pulido et al., 2007), or the opportunistic algae disappear over time, resulting in the restoration of healthy coral reefs.

The present paper focuses on remarkable pantropical monotypic blooms on coral reefs following catastrophic events, involving species in the coenocytic green algal genus *Trichosolen* (Bryopsidales, Chlorophyta; figure 1). This genus belongs to the *Pseudobryopsis*/*Trichosolen* (*PT*) complex.

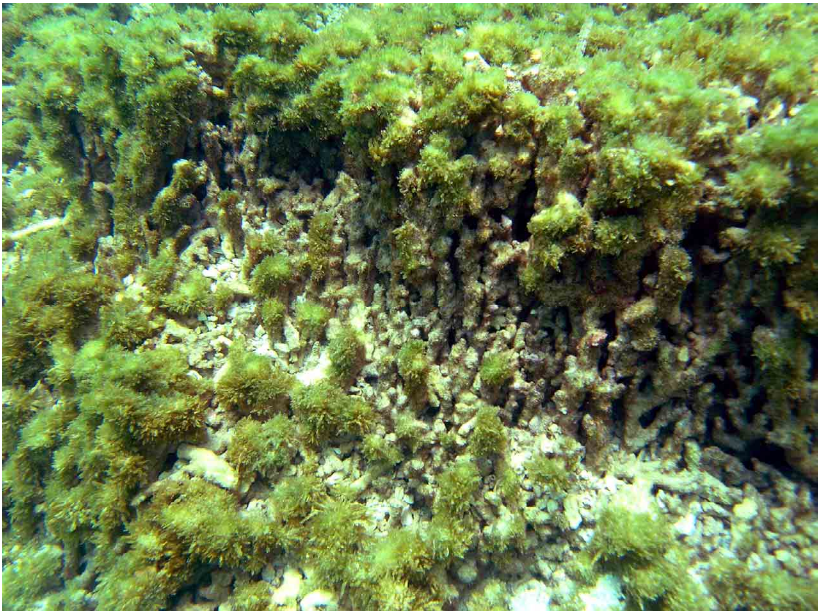

Figure 1. Mechanically damaged *Pocillopora damicornis* colonies at Fahal Island (Muscat, Oman) covered by a *Trichosolen* sp. bloom on 11 July 2007, five weeks after Cyclone Gonu in the Gulf of Oman. The picture depicts an area 1m across.

Species belonging to *Trichosolen* have often been attributed to *Pseudobryopsis* or vice versa, based on variable combinations of morphological and anatomical characters. The complex was revised by Henne & Schnetter (1999), who segregated the genera based on the presence or absence of a basal plug in the gametangia and pyrenoids in the chloroplast. Since *PT* species usually grow inconspicuously and are characterized by a partly microscopic life-cycle, worldwide distribution patterns of both *Pseudobryopsis* and *Trichosolen* remained largely elusive. Based on the revision of Henne and Schnetter (1999), distribution patterns emerged on a generic level, with *Pseudobryopsis* characterized by a subtropical and warm-temperate distribution accounting for the highest latitudes of the *PT* complex (including the Mediterranean Sea, Japan, eastern South Africa and southern Australia), while *Trichosolen* appears to have a more tropical worldwide distribution. Hence, most of the *PT* species reported to grow on coral reef systems are *Trichosolen*, some of which were exclusively found on coral. Moreover, within the complex, only *Trichosolen* has been documented to smother corals following physical damage. Woodley et al. (1981) were the first to report extensive blooms of *T. duchassaingii* one week after hurricane Allen hit Jamaican coral reefs in August 1980. Similarly, Littler et al. (1987) observed rapid colonisation by *T. molassensis* (a previously undescribed species) following the grounding of the freighter Wellwood on Molasses Reef in the Key Largo National Marine Sanctuary (Florida, US) in August 1984. Later, Littler and Littler (1999) described an extensive bloom of *Trichosolen* sp. on impacted corals on the Great Astrolabe Reef (Fiji) within 2-3 days after cyclone Gavin in March 1997. Lastly, a remarkably similar *Trichosolen* sp. bloom occurred on broken coral colonies and rubble immediately following cyclone Gonu in the Gulf of Oman in June 2007 (Jupp 2007, internal report but see Foster et al. (2008) and Wang & Zhao (2008) for reports on the cyclone and its biological consequences). All the blooms persisted for at least several weeks, and are in agreement with Littler & Littler's (1999) observations on the Florida and Fiji blooms: they are (1) monotypic, (2) widespread in time and space, (3) following severe physical impact, (4) persisting for weeks regardless of herbivore abundance, and (5) previously unknown from the sites despite elaborate prior floristic work.

Besides a sudden availability of suitable substrate, nutrient inputs originating from land-based run-off or sediment resuspension have been suggested as possible factors in the development of rapid overgrowths (Steneck & Dethier, 1994; Condie, 2009). Overall however, little (quantitative) information is available about the factors triggering such blooms because of a paucity of observations with relevant environmental data. This paper provides insights in the macroecological niche and the potential distribution of both blooming and non-blooming *Trichosolen* species growing on (damaged) coral reef systems, using a maximum entropy ecological niche modeling (ENM) technique based on known occurrence records and environmental layers related nutrient availability, sea surface temperature (SST) and coral distribution. An attempt is made to delineate key bloom risk areas and to identify environmental response optima for both non-bloom occurrences and bloom cases.

MATERIALS AND METHODS

SPECIES OCCURRENCE DATA

Literature and, where available, databases of publicly deposited specimens were searched for worldwide occurrence records of *Trichosolen* species sensu Henne & Schnetter (1999) reported to grow on coral reef systems, both in natural conditions and after disturbances. Subsequently, Google Earth was used to assign lat/long coordinates matching the locality descriptions as closely as possible in the case where no coordinates were mentioned. Occurrence records lacking sufficient geographical accuracy (e.g. only mentioning a country) were excluded for the ENM. The resulting 21 worldwide occurrence records (17 non-blooming records and 4 bloom cases, table 1) were manually checked for georeferencing errors against an administrative maritime boundaries map in Esri ArcGIS 9.2 and manually relocated where necessary to fall within sea areas, given the resolution of environmental data. Other data points such as *Trichosolen* records found on substrates outside coral reef systems or *Pseudobryopsis* records on coral reefs (representing a minority of the *PT* records previously often misreported as *Pseudobryopsis* and *Trichosolen* respectively) were retained for display in figure 2. A complete list of georeferenced *PT* records is shown in supplement S1.

Table 1. Records of *Trichosolen* occurring on coral reef systems used in the Maxent models. Bloom records are indicated in bold. The references are included in the general list at the end of this thesis.

Species (H&S '99)	Reported as	Source	Year	Country	Lat	Long
T. duchassaingii	*Bryopsis*	Taylor	1928	Florida	24.63	-82.93
T. duchassaingii	*Bryopsis*	Taylor	1960	Bahamas	24.5	-77.7
T. duchassaingii	*Bryopsis*	Taylor	1960	Barbados	13.2	-59.64
T. duchassaingii	*Trichosolen*	Richardson	1975	Trinidad	10.76	-61.44
T. duchassaingii	***Trichosolen***	**Woodley et al.**	**1981**	**Jamaica**	**18.47**	**-77.41**
T. duchassaingii	*Bryopsis*	Suárez	2005	Cuba	21.5	-79
T. gracilis	*Pseudobryopsis*	Womersley and Bailey	1970	Solomon	-8.75	158.07
T. gracilis	*Pseudobryopsis*	Coppejans et al.	2001	Papua N. Guinea	-4.77	145.7
T. molassensis	***Trichosolen***	**Littler et al.**	**1987**	**Florida**	**25.01**	**-80.37**
T. parva	*Pseudobryopsis*	Pham-Hoàng	1969	Vietnam	12.21	109.22
T. parva	*Pseudobryopsis*	Cribb	1984	Australia	-23.5	151.28
T. solomonensis	*Pseudobryopsis*	Womersley and Bailey	1970	Solomon	-8.45	158.13
T. solomonensis	*Pseudobryopsis*	Egerod	1975	Thailand	8.088	98.29
T. solomonensis	*Pseudobryopsis*	Egerod	1975	Thailand	7.803	98.41
T. solomonensis	*Pseudobryopsis*	Egerod	1975	Thailand	7.727	98.79
T. solomonensis	*Pseudobryopsis*	Egerod	1975	Thailand	7.745	98.74
T. solomonensis	*Pseudobryopsis*	Coppejans et al.	2001	Papua N. Guinea	-4.18	144.87
T. solomonensis	*Pseudobryopsis*	Coppejans et al.	2001	Papua N. Guinea	-5.13	145.82
T. sp.	*Trichosolen*	De Clerck & Coppejans	1996	Jubail	27.32	49.53
***T.* sp.**	***Trichosolen***	**Littler & Littler**	**1999**	**Fiji**	**-19.1**	**178.4**
***T.* sp.**	***Trichosolen***	**Jupp**	**2007**	**Muscat**	**23.68**	**58.5**

ENVIRONMENTAL DATA

Global SST and chlorophyll-a data (CHL, as a proxy for nutrient concentrations) available from the Aqua-MODIS satellite were assumed to be the major relevant ecophysiological variables driving survival and growth of *Trichosolen*. Three-monthly averaged (seasonal) level-3 pre-processed gridded maps for SST and CHL were downloaded at 5 arcmin (approximately 9 km) spatial resolution from OceanColor Web (http://oceancolor.gsfc.nasa.gov) and were subsequently cropped to include the highest latitudes at which *Trichosolen* is found to grow on coral reef systems (33°N-33°S). Raw pixel values (16bit) were recalculated to °C and mg m^{-3} using the respectively linear and exponential scaling equations provided in the metadata of the downloaded files. A uniform landmask was applied to all maps, masking out all freshwater bodies. These temporally averaged maps were not used as environmental variables for the modeling process as such. Instead, the following biologically meaningful variables were included, calculated using Clark Labs Idrisi Andes and Perl scripts: minimum, maximum, range and mean CHL (CHLmin, CHLmax, CHLrng and CHLavg) and SST (SSTmin, SSTmax, SSTrng and SSTavg). Additionally, as Schils & Wilson (2006) identified the average SST of the three warmest seasons as a powerful variable in explaining macroalgal biogeographical patterns, this variable was also included (SSTavg3warm). Two approaches were taken to reduce data redundancy using Idrisi Andes, as this can bias interpretation of the response curves in the niche modeling step. First, an unstandardized principal component analysis (PCA) was performed on the variables, and the first 3 PC grids (accounting for 99.58% of the overall variance) were used as environmental variable input in the ENM. This approach was adopted to produce the most accurate ENM maps while keeping the loss of information at a minimum (Verbruggen et al., 2009). Second, a subset of variables was selected based on a correlation analysis (Riordan & Rundel, 2009), and this subset was used to model environmental response curves. This approach may lead to a reduction of data but allows for easy interpretation of the resulting response curves, as opposed to using principal components. SStavg3warm and the two remaining least correlated variables per category (SSTmin, SSTrng, CHLmin and CHLrng; Pearson correlation, $0.48 < r < 0.8$) were retained for analyses in order to estimate the position of the niche in environmental space. Other potentially relevant variables available from OceanColor Web such as photosynthetically available radiation (PAR) and diffuse attenuation (DA, a measure of turbidity) are strongly correlated ($r > 0.8$) with SST and CHL, respectively, and were therefore not included.

Using ArcGIS 9.2, environmental data were extracted for all *Trichosolen* occurrences found on coral systems for subsequent multivariate analyses. Kruskal-Wallis tests were carried out in Statsoft Statistica 7 using the subset of five least-correlated variables as independent variables in order to evaluate different ecological characteristics of blooms and non-bloom records.

ENM

Because of the rarity, small size and semi-cryptic life-cycle of *Trichosolen* and the resulting lack of reliable absence data, a presence-only niche modeling algorithm was required. Therefore, Maxent v3.3.2, a software implementation based on the maximum entropy principle (Phillips et al., 2006; Phillips & Dudík, 2008) was used to model the potential distribution of *Trichosolen* on coral reefs and to assess the species' response to the environmental variables. The maximum entropy algorithm is a general-purpose method to infer a probability distribution from incomplete information. This probability distribution is most uniformly spread out (showing the highest degree of entropy) given the constraints represented by the environmental data observed at the given occurrence localities. Besides the raw environmental data input, Maxent also calculates transformations and interactions of these variables (so-called features) to constrain the distribution. Eventually, unlike other algorithms, Maxent converges to a unique, least-biased solution in estimating the unknown distribution. The resulting probability distribution is then translated from ecological space into geographical space. In the so-called logistic format, the output map shows pixel values ranging from 0 to 1, indicating niche suitability. Elith et al. (2006) have shown Maxent to perform well in comparison to other niche modeling algorithms, and Pearson et al. (2007) demonstrated that Maxent was able to model species' potential distributions based on as few as 5 to 25 occurrence records more accurately than other presence-only modeling algorithms such as GARP.

Maxent uses a large random sample of background environmental data (potentially including occurrence pixels, as opposed to generating pseudo-absences) to model the potential niche relative to the available environment. Most studies let Maxent randomly take 10000 points from the entire study area (a default option in the software). However, Phillips et al. (2009) pointed out that presence-only occurrence data often show a spatial sampling bias. This is often translated in an environmental sampling bias which, when combined with an evenly distributed background sample, leads to inaccurate models. To account for spatial sampling bias, background points with the same kind of bias as the occurrence records were selected: using Hawth's analysis tools for ArcGIS (Beyer, 2004), 10000 background points were randomly sampled only from the first two pixels adjacent to the landmask in the study area, so as to approximate a typical coastal sampling bias. Other model training parameters were left at their default settings (convergence threshold = 10^{-5}, maximum iterations = 500, automatic feature selection). Response curves of the modeled species to each of the 5 selected variables were also modeled by the Maxent algorithm.

The resulting continuous probability map based on the model using principal components as environmental variables was converted to a discrete map using two different thresholds to facilitate ecological interpretation. A 10th percentile training presence threshold was used to visualize the potential distribution of the macroecological niche of *Trichosolen* species growing on coral reef systems, while accounting for some potential uncertainty in occurrence data input. In order to delineate bloom risk areas, a more stringent fixed threshold of 0.8 was applied to the logistic suitability map. This threshold was chosen because VanDerWal et al. (2009) have shown that a suitability value at a given pixel is correlated with the maximum achievable biomass at that pixel, and as such a high suitability value represents a pixel where a bloom could potentially be sustained. In order to refine the macroecological niche distribution map to incorporate habitat suitability, the resulting discrete model output map was overlaid with 16700 coral distribution data points down to 40 m depth downloaded from ReefBase (Tupper et al., online publication) for which a 3-pixel buffer was created prior to raster conversion.

While a suitability map was modeled for all *Trichosolen* occurrence records on coral reefs, response curves were modeled both jointly and separately for blooms and non-blooms to gain insight in their ecology, i.e., blooms, non-blooms and all *Trichosolen* records on coral reef systems were treated as distinct "species" in the modeling process. The model based on all occurrences on coral systems was created to make full use of all possible data in examining the worldwide potential niche, as blooms necessarily develop from already present (although previously unnoticed) life stages. In contrast, the separate models for blooms and non-bloom cases were created to evaluate whether conditions specific for developing blooms could be distilled from the data.

MODEL EVALUATION

Models were run using approximately 75% of the occurrence records as training points and 25% as independent test points. Threshold-independent receiver operating characteristic (ROC) analysis allowed for model performance evaluation. The ROC curve plots the proportion of correctly predicted presences against the fractional area predicted present (in the case of presence-only models). The measure of predictive performance is the area under the ROC curve (AUC), varying between 0 and 1, where values above 0.5 (the area under the null expectations line) are indicative of models better than random. A four-fold cross-validation was implemented in order to obtain a standard deviation for the AUC values.

RESULTS

TRICHOSOLEN POTENTIAL DISTRIBUTION

The AUC values of the resulting Maxent model based on all *Trichosolen* occurrences on coral reef systems and principal components as environmental variables (table 2) indicate adequate model performance without overfitting to training data. The map shows a worldwide tropical to subtropical distribution of the macroecological niche (figure 2, global map), excluding cool waters (e.g. the Arabian Sea). When applying the 10th percentile training presence threshold (suitability value = 0.296) to the cross-validation replicate with the highest test AUC (0.969), the model was found to predict significantly better than random (p = 0.00003), with no records used for modeling falling outside the predicted suitable area (figure 2 selected regions: all open circles and stars fall within one of the four suitably colored areas). Although most of the macroecologically suitable areas are not located on coral reef systems with suitable substrate (dark green and yellow in figure 2), some other *Trichosolen* records have been found there (open triangles) as well as *PT* records of uncertain generic identity (filled circles). Narrowing down the distribution of the macroecological niche to areas where coral reef systems are present (orange and red in figure 2) results in the identification of several reef areas where *Trichosolen* has not yet been recorded, such as Costa Rica and Panama, the Red Sea and the Maldives, northeast Malaysia and the Philippines and Queensland (Australia). Areas with a suitability value exceeding 0.8 combined with coral availability (red pixels) represent the true bloom risk areas and cover all the recorded blooms.

Table 2. Area under the ROC curve (AUC) values of all Maxent model runs.

Model	Variables	N(train) per crossval run	AUC train mean (± SD)	N(test) per crossval run	AUCtest mean (± SD)
All *Trichosolen* on coral	PCA	16	0.958 (± 0.007)	5	0.945 (± 0.02)
All *Trichosolen* on coral	selected	16	0.942 (± 0.012)	5	0.922 (± 0.067)
Non-blooms	selected	13	0.916 (± 0.013)	4	0.837 (± 0.16)
Blooms	selected	3	0.845 (± 0.091)	1	0.804 (± 0.114)

ENVIRONMENTAL RESPONSE CURVES FOR *TRICHOSOLEN* ON CORAL

Kruskal-Wallis tests failed to reveal a significant difference between environmental variables for bloom or non-bloom occurrences found on coral reef systems (table 3). The Maxent model based on all *Trichosolen* occurrences on coral reefs and the subset with the 5 least correlated environmental variables performed only slightly worse for the training and test records, hence indicating a marginally lower predictive performance compared to the model based on principal components (table 2). The separate models for blooms and non-blooms have progressively lower AUC values. Although still indicating a better performance than random predictions, this effect is probably due to the low number of occurrence records (only 4 in the case of blooms). Rather than producing accurate maps, this approach is used here to analyze environmental variable response curves, summarized in figure 3. Response curves for SSTavg3warm, SSTmin and SSTrng exhibit a similar pattern across the models for all *Trichosolen* on coral systems, non-blooming occurrences and blooms, in favor of the warmest temperatures but with a tolerance for high ranges. Models for all *Trichosolen* records on coral reef systems and non-blooms correspond in the response curves for CHLmin and CHLrng, suggesting high support for the most oligotrophic conditions, corresponding to Jerlov class I oceanic waters. However, the model for blooms shows no response to CHLmin, while indicating an elevated response for an elevated CHLrng.

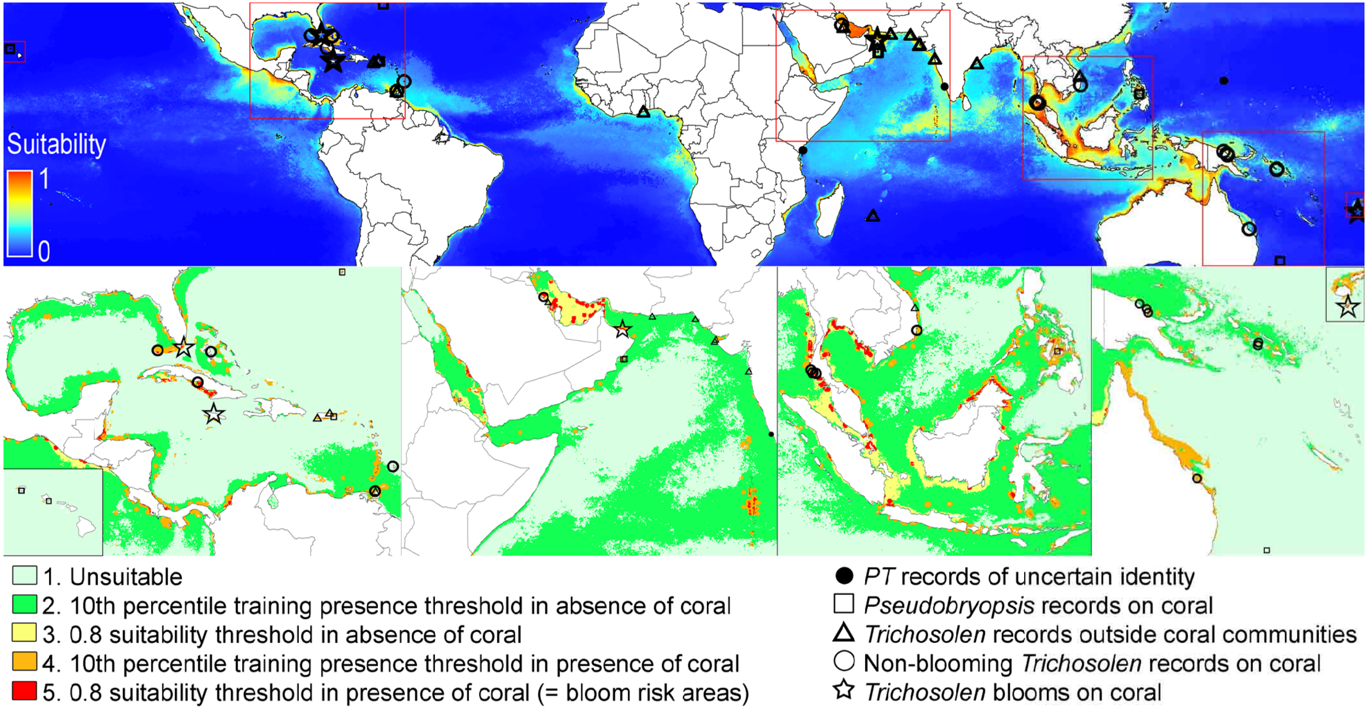

Figure 2. Niche suitability map based on all Trichosolen occurrences on coral and principal components as environmental variables. The global continuous probability map shown above represents the median suitability values derived from the 4 crossvalidation runs. Selected regions indicated by the red boxes are shown below from west to east, converted to discrete maps based on the 10th percentile training presence threshold, the 0.8 threshold and coral distribution data. Note that some occurrence symbols may overlap each other or cover colored pixels due to their size in this representation.

Table 3. Results of Kruskal-Wallis tests showing the difference between the environmental characteristics of all Trichosolen on coral reef systems, blooms and non-blooming occurrences.

	All *Trichosolen* on coral (N=21)	**Non-blooms (N=17)**	**Blooms (N=4)**	
Variable	mean (± SD)	mean (± SD)	mean (± SD)	**p**
CHLmin (mg m^{-3})	0.51 (± 0.71)	0.53 (± 0.78)	0.37 (± 0.21)	0.98
CHLrng (mg m^{-3})	0.97 (± 1.43)	0.9 (± 1.41)	1.39 (± 1.68)	0.84
SSTmin (°C)	25.94 (± 3.07)	26.23 (± 3.29)	24.72 (± 1.57)	0.39
SSTrng (°C)	4.61 (± 2.93)	4.45 (± 3.08)	5.44 (± 2.17)	0.44
SSTavg3warm (°C)	29.11 (± 2.74)	28.56 (± 2.09)	32.01 (± 4.17)	0.36

DISCUSSION

In recent years, ENM has been suggested as an effective, promising means to investigate species' biogeographical patterns and potential distribution, especially when occurrence records are scarce and reliable absence data cannot be obtained (Soberón & Peterson, 2004; Bentlage et al., 2009). This makes ENM a suitable tool for the investigation of ephemeral aquatic blooms which, by nature, offer limited sampling possibilities. Ephemeral macroalgal blooms on coral reefs have been reported to occur throughout the tropics, but the conditions enabling the formation of blooms often remain unclear (Burgess, 2006; Vroom et al., 2009). The bloom-forming species are usually known to be present in low abundances prior to the actual bloom formation. By contrast, *Trichosolen* bloom records were the only data source for some regions despite earlier floristic work around the bloom sites, probably because the present populations were in the microscopic part of the life cycle.

The failure of the Kruskal-Wallis tests to distinguish between blooms and non-blooming *Trichosolen* occurrences on coral reef systems based on the selected environmental variables illustrates the limitations of classical biogeographical approaches when few data are available. In contrast, different environmental responses are apparent for modeled blooms and non-blooming occurrences, while AUC values are acceptable for all these models. The apparent optima in the response curves are in agreement with the observed values (table 3), and support these data in a more reliable and quantitative way.

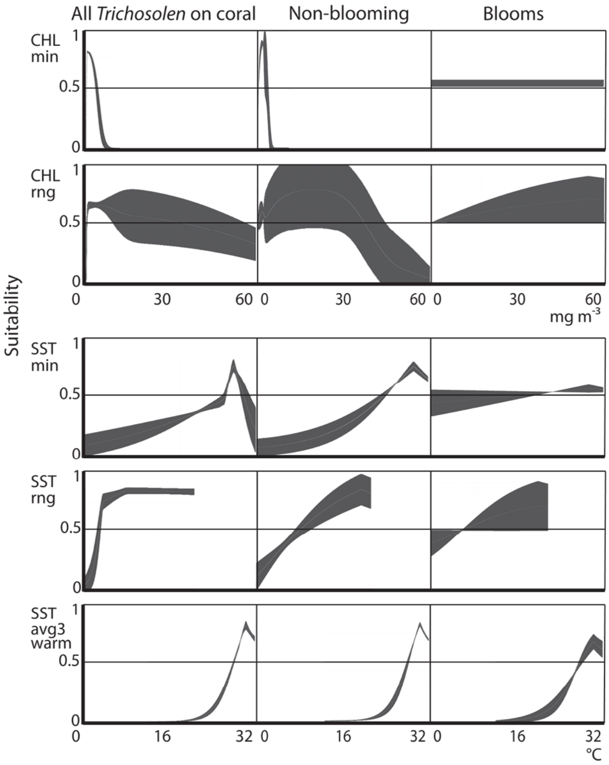

Figure 3. Response curves to the least-correlated environmental variables calculated by Maxent. Niche suitability ranges from 0 to 1 on the y-axis, while the range of environmental variables is shown on the x-axis. Response curves in the left column are based on all *Trichosolen* records on coral reef systems; the centre column shows response curves based on non-blooming records only; models based on bloom records only are shown in the right column. Environmental variable acronyms are listed in the materials & methods section. The light grey centre line represents the median value derived from the 4 crossvalidation runs, while the dark grey band delineates the standard deviation.

A first condition for blooms to develop is a sudden availability of suitable substrate (dead or cleared surfaces on coral reef systems) through a mechanically damaging event. Second, the peak at low concentrations in the CHLmin response curve for the models based on all occurrences and non-blooming *Trichosolen* on coral reefs, combined with the response optima for a low to intermediate CHLrng, demonstrates a preferred occurrence of *Trichosolen* in clear, oligotrophic waters. These are mostly tropical waters, since the response curve of all models to SSTmin favors the highest values. On the other hand, the lack of response for bloom cases to CHLmin and an increasing tolerance towards elevated CHLrng values indicate that blooms are more likely to occur in areas where chlorophyll concentrations can peak to extreme values (beyond seasonal fluctuations, i.e. on rare events), whereas non-blooming *Trichosolen* occurrences are more likely to be restricted to areas with continuously low chlorophyll concentrations. Moreover, the oceanographic observations by Wang & Zhao (2008) suggest the importance of sudden nutrient inputs caused by cataclysmic events, e.g. by sediment resuspension. In fact, peak nutrient concentrations during and shortly after these events might be an important factor besides available substrate and a reduction in herbivore density for *Trichosolen* to develop into a bloom. Thirdly, since the response curves of all *Trichosolen* models to SSTavg3warm favor the highest temperatures, *Trichosolen* growth and blooms are most likely to occur in areas characterized by an average temperature during the three warmest seasons that exceeds 28 °C (characteristic of tropical floras, see Schils & Wilson (2006)). Moreover, the confidence intervals of SSTavg3warm are very small, indicating the explanatory power of this variable. Since all the blooms were exclusively observed in the hottest season, this also suggests that this is the risk season. However, since the response of *Trichosolen* blooms to SSTmin is less pronounced than that of normal occurrence events, it could be hypothesized that blooms may also develop following a catastrophic event with sudden nutrient input even when the SST is suboptimal, whereas otherwise the background population (present in the microscopic part of the life cycle) would not develop in macroscopic growth before optimal temperatures are reached when the water column is oligotrophic.

The discrete maps in figure 2 show the geographical distribution of the macroecological niche of *Trichosolen* based on the thresholds discussed above, while isolating areas within its niche that also feature a suitable habitat (shallow coral substrate). Only areas with both a higher than 0.8 niche suitability value and the presence of coral reef systems are delineated as bloom risk areas which could be prioritized for targeted bloom monitoring when damaging events occur on the reefs. Likewise, other macroecologically suitable areas coinciding with coral reef presence (orange) might be used to guide exploration of new populations to expand biogeographical knowledge of the genus *Trichosolen*. From these maps, it is also apparent that habitat suitability is often controlled at a fine spatial scale, for which the resolution of the present model may not always be sufficient (illustrated by isolated suitable pixels around reef islands). For guidance of field work, it is important to note that biotic and abiotic microhabitat variables such as wave exposure and grazing pressure could evidently not be incorporated in a modeling effort at a global scale. To further refine similar modeling efforts, coral reef impact variable maps might be included at different scales (post-hoc); these could include meteorological variables such as cyclone frequency and intensity, shipping intensity as a proxy for ship grounding risk (Halpern et al., 2008), and *Acanthaster* distribution maps.

Besides the selection of the modeling algorithm, some measures were taken in order to optimize the modeling process based on a low number of occurrence data. This study addresses the algorithm's sensitivity to sample selection bias by adopting a target-group background selection which is likely to show the same environmental bias as in the species occurrence data. Table 4 shows that the spread of environmental data for the occurrence records reasonably matches the averaged spread of background environmental data in ecological space (although less for CHL extremes). Additionally, suitability maps were modeled using principal components as environmental variables to ensure model performance was not affected by data redundancy. Raw variables were used to calculate environmental response curves for pragmatic reasons in interpreting the results, but again data redundancy was avoided by selecting the least correlated variables. Burgess (2006) noted that ephemeral blooms on tropical reef systems might be far more widely spread in time and space than currently observed, and stressed that the paucity of distributional and water quality data hampered understanding of the factors related to these blooms.

Table 4. Overview of the spread in ecological space of occurrence records compared to the target-group selected background data.

	All *Trichosolen* on coral (N=25)			**Target-group background (N=10000)**		
Variable	min	max	mean (± SD)	min	max	mean (± SD)
CHLmin (mg m^{-3})	0.06	1.87	0.42 (± 0.48)	0.01	64	1.84 (± 3.01)
CHLrng (mg m^{-3})	0.04	8.8	1.05 (± 1.43)	0	64	3.03 (± 5.96)
SSTmin (°C)	18.68	29.12	25.94 (± 3.07)	5.92	30.59	24.61 (± 4.45)
SSTrng (°C)	1.68	14.59	4.66 (± 2.93)	0.48	23.19	5.25 (± 3.74)
SSTavg3warm (°C)	25.72	30.62	29.11 (± 2.74)	14.67	36	29.44 (± 3.35)

The approach outlined in this paper yielded quantitative ecological information based on few occurrence records and can potentially be used to shed new light on similar ephemeral blooms, which are known to be increasing in frequency and intensity with global change (Rabalais, 2009).

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SUPPLEMENTARY MATERIAL

S1. Complete list of georeferenced *PT* records.

GENUS (H&S '99)	SPECIES	REPORTED AS	AUTHOR/HERBARIUM	YEAR	COUNTRY/REGION	ECOLOGICAL REMARKS	LAT	LONG
Pseudobryopsis	*blomquistii*	*Pseudobryopsis*	Diaz-Piferrer	1965	Puerto Rico	on dead coral, 10-15m	18.1100	-65.5870
Pseudobryopsis	cf. *hainanensis*	*Trichosolen*	Norris	1992	South Africa/KZN	in intertidal rock pools on reef	-26.8833	32.8833
Pseudobryopsis	cf. *hainanensis*	*Trichosolen*	Norris	1992	South Africa/KZN	in intertidal rock pools on reef	-28.1333	32.5667
Uncertain	cf. *P. mucronata*	*Trichosolen*	Vandenheede	1994	Kenya	on wall of lower intertidal rock pool	-4.0550	39.7060
Trichosolen	*duchassaingii*	*Trichosolen*	Woodley	1981	Jamaica	on shallow corals after hurricane	18.4700	-77.4100
Trichosolen	*duchassaingii*	*Bryopsis*	Taylor	1960	Bermuda	*no locality information*	32.3100	-64.8000
Trichosolen	*duchassaingii*	*Bryopsis*	Taylor	1928	Florida	*no ecological remarks*	24.6290	-82.9300
Trichosolen	*duchassaingii*	*Bryopsis*	Taylor	1960	Bahamas	*no locality information*	24.5000	-77.7000
Trichosolen	*duchassaingii*	*Bryopsis*	Taylor	1960	Barbados	*no locality information*	13.2000	-59.6400
Trichosolen	*duchassaingii*	*Bryopsis*	Suárez	2005	Cuba	*no locality information*	21.5000	-79.0000
Trichosolen	*duchassaingii*	*Trichosolen*	Richardson	1975	Trinidad	rare; intertidall rock pool; under shallow rock ledge	10.7600	-61.4350
Trichosolen	*gracilis*	*Pseudobryopsis*	Coppejans	2001	PNG	on coral rubble between reef flat & inner slope, 3m	-4.7667	145.7000
Trichosolen	*gracilis*	*Pseudobryopsis*	Womersley	1970	Solomon	on stones in calm water	-8.7500	158.0667
Pseudobryopsis	*hainanensis*	*Trichosolen*	GENT (unpubl.)	1999	Oman/Masirah East	on shallow coral heads; on sandy stones, 11m	20.2730	58.7800
Pseudobryopsis	*hainanensis*	*Pseudobryopsis*	Tseng	1936	China/Hainan	on intertidal stem of *Rizophora* sp.	19.4800	110.8000
Pseudobryopsis	*hainanensis*	*Trichosolen*	Yoshida	1995	Japan/Oki	*no locality information*	36.2480	133.3760
Pseudobryopsis	*hainanensis*	*Pseudobryopsis*	Kraft	2007	Australia/LHI	in turf assemblage on coral bommies, 7-21m	-31.5090	159.0650
Pseudobryopsis	*hainanensis*	*Pseudobryopsis*	Huisman	2003	Australia/Western	*no locality information*	-20.6620	116.7000
Pseudobryopsis	*hainanensis*	*Pseudobryopsis*	Huisman	2000	Australia/Western	*no locality information*	-28.7000	113.8000
Pseudobryopsis	*hainanensis*	*Pseudobryopsis*	Huisman	2000	Australia/Western	*no locality information*	-31.9900	115.5600
Pseudobryopsis	*hainanensis*	*Pseudobryopsis*	Millar	1994	Australia/NSW	only on islands in NSW	-30.2400	153.1790
Trichosolen	*longipedicellata*	*Psuedobryopsis*	Blomquist	1961	Puerto Rico	*no ecological remarks*	18.5000	-66.0000
Trichosolen	*longipedicellata*	*Psuedobryopsis*	Blomquist	1961	Puerto Rico	*no ecological remarks*	18.0000	-67.2000
Trichosolen	*mauritianus*	*Pseudobryopsis*	Boergesen	1948	Mauritius	free-floating after storm	-20.1667	57.4833
Trichosolen	*mauritianus*	*Trichosolen*	Basson	1979	Saudi-Arabia	on pier	26.7000	50.1000
Trichosolen	*molassensis*	*Trichosolen*	Littlers	1987	Florida	on coral after ship grounding	25.0117	-80.3733
Trichosolen	*mucronatus*	*Pseudobryopsis*	Pham-Hoang	1969	Vietnam	*no locality information*	14.5800	109.0820
Trichosolen	*mucronatus*	*Pseudobryopsis*	Umamaheswararao	1970	India/Visakhapatnam	on sand-covered rocks	17.7187	83.3365
Trichosolen	*mucronatus*	*Pseudobryopsis*	Srinivasan	1969	India/S Gujarat	on walls of intertidal rock pools; in shallow subtidal	22.4790	69.0755
Trichosolen	*mucronatus*	*Pseudobryopsis*	Srinivasan	1969	India/N Gujarat	on walls of intertidal rock pools; in shallow subtidal	22.2385	68.9577
Trichosolen	*mucronatus*	*Pseudobryopsis*	Boergesen	1930	India/Bombay	in shallow water	18.8920	72.8080
Trichosolen	*mucronatus*	*Trichosolen*	Shameel	1996	Pakistan/Makran	subtidal benthic drift	25.0865	61.8630
Trichosolen	*mucronatus*	*Pseudobryopsis*	Shameel	1992	Pakistan/Karachi	benthic subtidal	24.8415	66.7745
Pseudobryopsis	*myura*	*Pseudobryopsis*	Wynne	2001	Oman/Dhofar	in sand in exposed bay, 8.5m	17.0052	54.0153
Pseudobryopsis	*myura*	*Pseudobryopsis*	Rayss	1955	Israel	in deep shaded calm tide pools	33.0649	35.1039
Pseudobryopsis	*myura*	*Trichosolen*	GENT (unpubl.)	1976	Turkey/South	*no ecological remarks*	36.2663	30.1420
Pseudobryopsis	*myura*	*Trichosolen*	Ballesteros	1990	Spain/Catalonia	*no locality information*	42.3190	3.3225
Pseudobryopsis	*myura*	*Pseudobryopsis*	Meñez	1987	Tunisia	occasional; in April and May on subtidal rocks	33.7900	11.0600
Pseudobryopsis	*myura*	*Pseudobryopsis*	Feldmann	1929	France/Southeast	some years only, restricted to August-September	42.4760	3.1560
Pseudobryopsis	*myura*	*Trichosolen*	GENT (unpubl.)	1974	France/Southeast	*no ecological remarks*	43.0060	6.3765

S1. (continued)

GENUS (H&S '99)	SPECIES	REPORTED AS	AUTHOR/HERBARIUM	YEAR	COUNTRY/REGION	ECOLOGICAL REMARKS	LAT	LONG
Pseudobryopsis	*myura*	*Trichosolen*	GENT (unpubl.)	1975	France/Southeast	*no ecological remarks*	43.4118	6.8534
Pseudobryopsis	*myura*	*Trichosolen*	GENT (unpubl.)	1976	France/Corsica	*no ecological remarks*	42.5835	8.7250
Pseudobryopsis	*myura*	*Trichosolen*	Giaccone	1985	Italy/W Sicily	intertidal; subtidal	38.0200	12.5000
Pseudobryopsis	*myura*	*Trichosolen*	Giaccone	1985	Italy/N Sicily	intertidal; subtidal	38.4200	14.9500
Pseudobryopsis	*myura*	*Trichosolen*	Giaccone	1985	Italy/E Sicily	intertidal; subtidal	37.5600	15.1660
Pseudobryopsis	*myura*	*Trichosolen*	Giaccone	1985	Italy/E Sicily	intertidal; subtidal	37.0600	15.3000
Pseudobryopsis	*myura*	*Pseudobryopsis*	Haroun	2002	Canary Ils	*no locality information*	28.1500	-15.5000
Pseudobryopsis	*myura*	*Pseudobryopsis*	Haroun	2002	Canary Ils	*no locality information*	29.3000	-13.5000
Pseudobryopsis	*myura*	*Trichosolen*	Phillips	1997	Australia/Queensland	*no locality information*	-23.4830	151.2350
Pseudobryopsis	*myura*	*Trichosolen sp.*	GENT (unpubl.)	2006	Madeira	on large round boulders, 6-9m	32.6357	-16.9360
Pseudobryopsis	*oahuensis*	*Pseudobryopsis*	Abbott	2004	Hawaii/Oahu	in sand or on eroded coral, high intertidal to 5m	21.2530	-157.8100
Pseudobryopsis	*oahuensis*	*Pseudobryopsis*	GUAM (unpubl.)	1959	Hawaii/Oahu	growing on wave-washed bench with Gelidium	21.2687	-157.6920
Pseudobryopsis	*oahuensis*	*Pseudobryopsis*	GUAM (unpubl.)	1959	Hawaii/Oahu	in rapid current, 0-2m; on vertical concrete pier	21.2728	-157.8303
Pseudobryopsis	*oahuensis*	*Pseudobryopsis*	GUAM (unpubl.)	1959	Hawaii/Kauai	*no ecological remarks*	21.8785	-159.4779
Pseudobryopsis	*pambanensis*	*Pseudobryopsis*	Iyengar	1938	India/S	*no locality information*	9.2750	79.2040
Pseudobryopsis	*papillata*	*Trichosolen*	Papenfuss	1968	Egypt/Red Sea	*no locality information*	27.7500	34.2200
Trichosolen	*parva*	*Pseudobryopsis*	Pham-Hoang	1969	Vietnam	on surface of dead coral, 2-3m	12.2110	109.2170
Trichosolen	*parva*	*Pseudobryopsis*	Cribb	1984	Australia/Queensland	*no ecological remarks*	-23.5300	151.2800
Trichosolen	*retrorsa*	*Trichosolen*	John	1977	Ghana	on cobbles in waves	5.6750	0.1217
Trichosolen	*solomonensis*	*Pseudobryopsis*	Coppejans	2001	PNG	on strongly insolated sand covered reef flat, 1.5m	-4.1833	144.8667
Trichosolen	*solomonensis*	*Pseudobryopsis*	Coppejans	2001	PNG	on slightly sand covered coral on reef flat, 1.5m	-5.1333	145.8167
Trichosolen	*solomonensis*	*Pseudobryopsis*	Womersley	1970	Solomon	on acropora in waves	-8.4500	158.1333
Trichosolen	*solomonensis*	*Pseudobryopsis*	Egerod	1975	Thailand	on intertidal sandy coral	8.0875	98.2900
Trichosolen	*solomonensis*	*Pseudobryopsis*	Egerod	1975	Thailand	on silted slate on coral in upper intertidal	7.8030	98.4110
Trichosolen	*solomonensis*	*Pseudobryopsis*	Egerod	1975	Thailand	in shady cove	7.7265	98.7900
Trichosolen	*solomonensis*	*Pseudobryopsis*	Egerod	1975	Thailand	on sandy coral, 2-3m	7.7445	98.7638
Trichosolen	sp.	*Trichosolen*	De Clerck	1996	Jubail	on dead coral, 2m	27.3147	49.5344
Trichosolen	sp.	*Trichosolen*	Littlers	1999	Fiji	on coral after cyclone	-19.0700	178.4000
Trichosolen	sp.	*Trichosolen*	Jupp	2007	Muscat	on coral after cyclone	23.6791	58.5013
Uncertain	sp.	*Trichosolen*	GENT (unpubl.)	2006	Spain/Catalonia	intertidal; shallow subtidal	41.8419	3.1279
Uncertain	sp.	*Trichosolen*	GUAM (unpubl.)	1989	Guam	on reef slope, ca. 10m	13.4223	144.7904
Uncertain	sp.	*Trichosolen*	GENT (unpubl.)	1999	Oman/Masirah West	on sand covered rockand coral heads, 5.5m	20.215	58.632
Uncertain	sp.	*Trichosolen*	GENT (unpubl.)	1998	Phillipines/Macan East	intertidal	10.301	124.0175
Uncertain	*thikkodiensis*	*Pseudobryopsis*	Anil Kumar	1993	India/Kerala	*no locality information*	11.5200	75.6000
Pseudobryopsis	*venezoleana*	*Trichosolen*	Ganesan	1990	Venezuela	*no locality information*	10.6100	-66.8930

Excluded: *Trichosolen planktonica; Pseudobryopsis hainanensis (Korea)*