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Niche Modelling: A comparison between Modelling Methods best applied for Cnidaria Niche Dispersion Studies

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Orientador: Sérgio Nascimento Stampar

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To my Mum, who was always there for me

Especially in the darker days

"Sometimes it's the people no one imagines anything of who do the things that no one can imagine."

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Chapter 1

Cnidaria Niche Modelling: A review

Abstract

The use of predictive modelling, or ecological niche modelling, has been increasing rapidly in the last decades. The applications to this tool are just as wide, with the possibility of using it for business projections or on biology fields. Regarding biological areas, it is becoming more important, once it can generate results otherwise impossible, if not for models, such as future distribution projections for species. Despite its wide range of applications, the aquatic environment still presents obstacles. Our aim here was to make a bibliographic research on papers published on open access websites regarding niche modelling on Cnidaria. Our results have shown that in much of those papers, sessile animals were used, and that most of them date from the year 2011, with the preference for the MAXENT algorithm. This can be explained by the fact that the software was developed on the XXI century with computers popularization. Our project also showed the potential for future improvements on this area and, as it was the first, it can serve as base for future researches.

Keywords: Modelling, Niche modelling cnidaria, Cnidaria.

1. INTRODUCTION

For a few decades, predictive modelling has been receiving more attention in mathematical and biological areas. In biology, we can find several applications, such as community assessment modelling (van der Molen, 2015; Jiang et al., 2007), genetic modelling, (Ruiz-Ramos, 2015), behavioural (Aktius, 2007), coral bleaching patterns (Williams et al., 2010) and specially, species distribution model (SDM) (Davies & Guinotte, 2011; Guinan et al., 2009; Tong et al., 2013).

Species distribution model or ecological niche models have been increasingly used in the last decade (Peterson et al., 2007). It started to be used for aquatic organisms in the beginning of the 20th century, when the method of statistical-mathematic analysis, focusing on invasive species, was applied with significant results (Hill et al., 1998). It is now pertinent to conservation, invasive species management, epidemiology and ecology (Welk et al., 2002; Peterson & Shaw, 2003; Phillips et al., 2006, Kearney & Porter, 2016).

Studies using ENM are, in its majority, focused on terrestrial fauna and flora (Wiley et al., 2003; Guinotte et al., 2006; Therriault & Herborg, 2008; Bentlage et al., 2009), not been so vastly applied for zooplankton possibly due to gaps of samples (Chust et al., 2014, Vallarino et al., 2015). Only on the 21st century, this modelling technique started to be applied for cnidarians, with an increase after 2011. This increase coincides with the development of more complex algorithms such as MAXENT (Phillips et al., 2004; 2006), Garp (Stockwell and Peters 1999) and ENFA (Hirzel et al., 2002).

One of the first articles based on marine invertebrates was in 2012, Meißner et al. modelled the distribution of several benthic invertebrates, including two Hydrozoa in the Iceland coast, aiming to stablish the study as base for future studies in similar regions. The results presented extreme changes in Antarctic and sub-Antarctic habitats due to climate change. Several papers used the same region to model the distribution of mammals, birds and fishes (Fløjgaard et al., 2009; Illoldi-Rangel et al., 2004; Moore and Huntington, 2008; Waltari & Guralnick, 2008).

Comparison of algorithms and assertion of one that produces best models are also the focus of several research groups, without a minimum consensus. Guinan et al. (2008) used GARP and ENFA to compare which would be the most reliable for modelling deep-sea corals. Brame and Stigal (2013) used GARP and MAXENT to model invertebrates' distribution in the late ordoviciane and Tittensor et al. (2009) modelled the global distribution for stony corals comparing ENFA and MAXENT. Yesson et al., 2012 were the first to create models of niches for octocorals, using MAXENT, these authors observed which abiotic data in the environment affected the most the development of these animals. The authors stress the importance of a continue research in this field.

There is a relevant field of research tending to focus on the identification of possible habitats for colonization of endangered or affected species (Bentlage et al., 2009; Tracey et al., 2011; Yesson et al., 2012; Tong et al., 2012; Guinotte et al., 2014). Evidently, this research kind are relevant for several other research fields on biodiversity as climate changes (Tracey et al., 2011) or invasive species (Carlos-Junior et al., 2015). In most of the cases, researchers use two or more algorithms in the process to compare their results pointing to the most reliable for specific groups (Guinan et al., 2008; Tittensor et al., 2009; Tong et al., 2012; Bentlage, 2013).

In the present study, we wanted to access which algorithm is the most used for modelling cnidarians, by performing a bibliographic review of the topic. Up to now, there is nothing in the literature with this purpose and this is the first study verifying the scenario of performed studies. Based on results this article can become base for future projects.

2. METHODOLOGY

The data for the systematic review were obtained from the Google Scholar (https://scholar.google.com), with the keywords "modelling cnidaria", "niche modelling cnidaria" in English, Spanish and Portuguese. This platform was used because this is the most accessible to do a reliable research from anywhere in the World and it is also the one with the broadest scope of the database.

Based on the results, we selected those relevant to our objectives, excluding those in which the model was not on cnidaria or was not based on niche ecology distribution. We considered, however, those that used statistical methods only as those that used specific algorithms without distinction of algorithm. We also considered the year of the publication, separating by decade from 1980 to 2016 in order to ascertain in what decade the tool became most popular, and what algorithm was used the most.

3. RESULTS

We obtained 578 articles, where after thorough analysis; we were able to remain with 93. From this total amount, only 5 were from 1991-2000, 33 were from the second decade, and 55 from 2011 to June 2016. This last decade presents an increase of 55% of publications with this topic (figure 1), and it also present MAXENT as the main algorithm used in niche modelling, with a prevalence of 53% over the other algorithms found (ENFA, R, GARP, BIOCLIM, AquaMaps, GLM, GAM and other mathematical models). If we consider only the data from the second decade, from 2001, MAXENT's use represented 36%, representing a clear preference for this algorithm (Figure 2).

We noticed that, every time GARP was used, it was associated with another algorithm, mainly MAXENT, and always comparing the both of them. This is not observed for ENFA, for example, algorithm that in only 22% of the cases was combined with MAXENT.

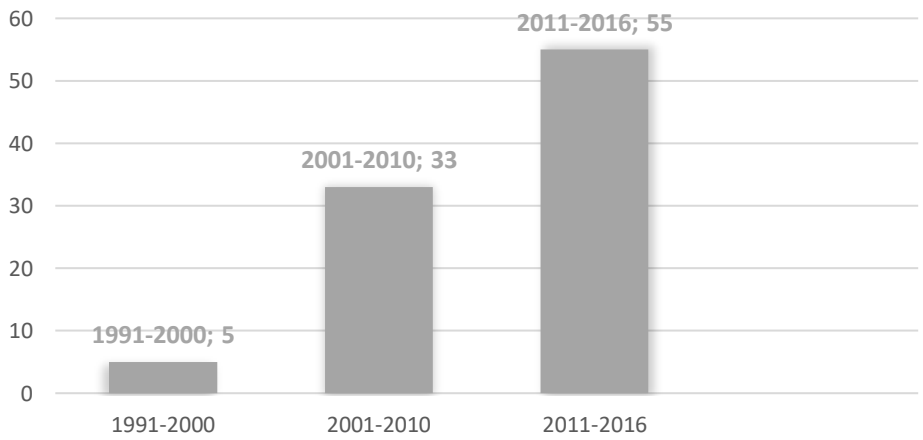

Figure 1│ Percentage of published articles from 1991 to June 2016 regarding cnidaria niche modelling. Publications are divided in decades to better represent the years in which there is a clear increase in using these tools.

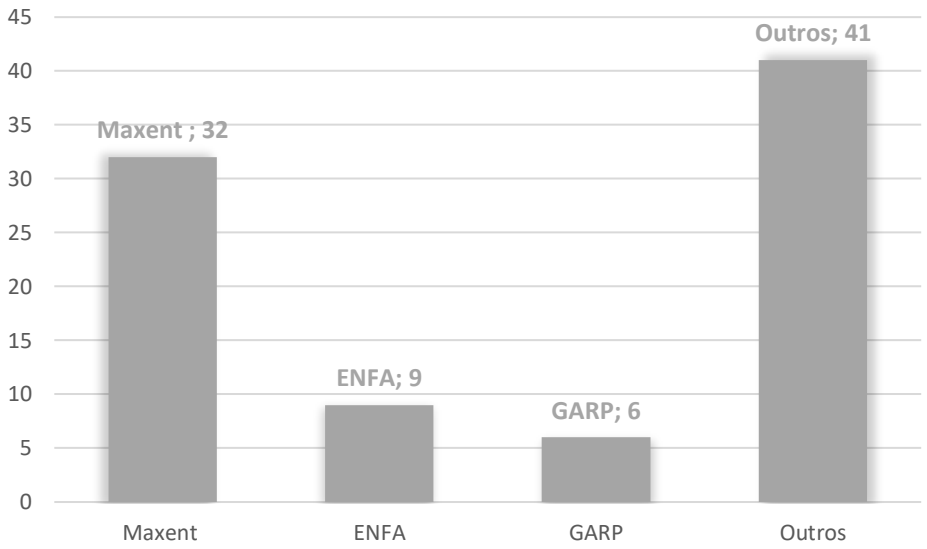

Figure 2│Comparison of the utilization of the algorithms found (MAXENT, GARP, ENFA, and "others" include R, GAM, GLM BIOCLIM, AquaMaps and mathematic models) for the years 2001 to June 2016.

4. DISCUSSION

The niche modelling, according to our research, began to be used in 1998. However, it became more popular only after the year 2000 and in the last 5 years there was a significant increase in its publications. It is unquestionable the preference for the MAXENT algorithm regarding the cnidaria group. Merow et al. (2014) also corroborate this data with over 2000 citations in the last 10 years for MAXENT, although not restricted to cnidarians, but involving several organisms.

Several papers aim to compare algorithms in order to assert the superior one, even though it is a risky strategy once each algorithm presents different aspects for the model itself (Jimenez-Valverde et al., 2008). Many studies, through the years, have been trying to present conclusive results about which algorithm is the most reliable, and the majority points to MAXENT (Brotons et al., 2004; Elith et al., 2006; Elith et al., 2010; Guinotte & Davis, 2014; Segurado &

Araujo, 2004; Tsoar et al., 2007). However, in the last few years, evidences have been piling up showing that MAXENT's results may not be reliable depending on the model selection criteria (Warren & Seifert, 2011). Morales et al., 2017 highly stress the need to access which papers are reliable and summarize important points to be taken in consideration before modelling. Using the jackknife procedure (Shcheglovitova & Anderson, 2013) and comparing the results obtained by the model and *in situ* results, may present a more reliable conclusion to one's paper.

Most papers related to this subject are focused on benthic animals from either shallow or deep water, and only one based on a planktonic species, Cubozoan jellyfish (Bentlage et al., 2009). This study presents data on influence of climate changes in Australia and stressing the necessity of more research of this sort for organisms still poorly known, like marine invertebrates.

The reduced amount of available data for several organisms leaves an information gap that modelling can help to fill. The small amount of distribution data found in the present study, show the importance of continuing studies with these animal niches, both to provide a general idea of their dispersion and to define the most reliable algorithm to use with animals from each phylum.

5. REFERENCES

Aktius, M., Nordahl, M., & Ziemke, T. (2007). A behavior-based model of the hydra, phylum Cnidaria. *Advances in Artificial Life*, 1024-1033.

Bentlage, B., Peterson, A. T., & Cartwright, P. (2009). Inferring distributions of chirodropid box-jellyfishes (Cnidaria: Cubozoa) in geographic and ecological space using ecological niche modeling. *Marine Ecology Progress Series*, *384*, 121-133.

Bentlage, B., Peterson, A. T., Barve, N., & Cartwright, P. (2013). Plumbing the depths: extending ecological niche modelling and species distribution

modelling in three dimensions. *Global Ecology and Biogeography*, *22*(8), 952-961.

Brame, H. M. R., & Stigall, A. L. (2014). Controls on niche stability in geologic time: congruent responses to biotic and abiotic environmental changes among Cincinnatian (Late Ordovician) marine invertebrates. *Paleobiology*, *40*(1), 70-90.

Brotons, L., Thuiller, W., Araújo, M. B., & Hirzel, A. H. (2004). Presence-absence versus presence-only modelling methods for predicting bird habitat suitability. *Ecography*, *27*(4), 437-448.

Carlos-Júnior, L. A., Neves, D. M., Barbosa, N. P., Moulton, T. P., & Creed, J. C. (2015). Occurrence of an invasive coral in the southwest Atlantic and comparison with a congener suggest potential niche expansion. *Ecology and evolution*, *5*(11), 2162-2171.

Chust, G., Castellani, C., Licandro, P., Ibaibarriaga, L., Sagarminaga, Y., & Irigoien, X. (2013). Are Calanus spp. shifting poleward in the North Atlantic? A habitat modelling approach. *ICES Journal of Marine Science: Journal du Conseil*, fst147.

Davies, A. J., & Guinotte, J. M. (2011). Global habitat suitability for framework-forming cold-water corals. *PloS one*, *6*(4), e18483.

Elith, J., Graham, C.H., Anderson, R.P., Dudı´k, M., Ferrier, S., Guisan, A.et al. (2006) Novelmethods improve prediction of species' distributions from occurrence data. Ecography, 29, 129–151.

Elith, J., Kearney, M., & Phillips, S. (2010). The art of modelling range-shifting species. *Methods in ecology and evolution*, *1*(4), 330-342.

Fløjgaard, C., Normand, S., Skov, F., & Svenning, J. C. (2009). Ice age distributions of European small mammals: insights from species distribution modelling. *Journal of Biogeography*, *36*(6), 1152-1163.

Greathead, C., González-Irusta, J. M., Clarke, J., Boulcott, P., Blackadder, L., Weetman, A., & Wright, P. J. (2014). Environmental requirements for three

sea pen species: relevance to distribution and conservation. *ICES Journal of Marine Science: Journal du Conseil*, fsu129.

Guinan, J., Brown, C., Dolan, M. F., & Grehan, A. J. (2009). Ecological niche modelling of the distribution of cold-water coral habitat using underwater remote sensing data. *Ecological Informatics*, *4*(2), 83-92.

Guinotte, J. M., & Davies, A. J. (2014). Predicted deep-sea coral habitat suitability for the US West Coast. *PloS one*, *9*(4), e93918.

Hengl, T., Sierdsema, H., Radović, A., & Dilo, A. (2009). Spatial prediction of species' distributions from occurrence-only records: combining point pattern analysis, ENFA and regression-kriging. *Ecological Modelling*, *220*(24), 3499-3511.

Hill, D., Coquillard, P., de Vaugelas, J., & Meinesz, A. (1998). An algorithmic model for invasive species: application to Caulerpa taxifolia (Vahl) C. Agardh development in the North-Western Mediterranean Sea. *Ecological modelling*, *109*(3), 251-266.

Hirzel, A. H., Hausser, J., Chessel, D., & Perrin, N. (2002). Ecological-niche factor analysis: how to compute habitat-suitability maps without absence data?. *Ecology*, *83*(7), 2027-2036.

Illoldi-Rangel, P., Sánchez-Cordero, V., & Townsend Peterson, A. (2004). Predicting distributions of Mexican mammals using ecological niche modeling. *Journal of Mammalogy*, *85*(4), 658-662.

Jiang, H., Cheng, H. Q., Xu, H. G., Arreguín-Sánchez, F., Zetina-Rejón, M. J., Luna, P. D. M., & Le Quesne, W. J. (2008). Trophic controls of jellyfish blooms and links with fisheries in the East China Sea. *Ecological Modelling*, *212*(3), 492-503.

Jiménez-Valverde, A., Lobo, J. M., & Hortal, J. (2008). Not as good as they seem: the importance of concepts in species distribution modelling. *Diversity and distributions*, *14*(6), 885-890.

Meißner, K., Fiorentino, D., Schnurr, S., Arbizu, P. M., Huettmann, F., Holst, S., ... & Svavarsson, J. (2014). Distribution of benthic marine invertebrates

at northern latitudes—An evaluation applying multi-algorithm species distribution models. *Journal of Sea Research*, *85*, 241-254.

Moore, S. E., & Huntington, H. P. (2008). Arctic marine mammals and climate change: impacts and resilience. *Ecological Applications*, *18*(sp2).

Morales, N.S., Fernández, I.C. and Baca-González, V., (2017). MAXENT's parameter configuration and small samples: are we paying attention to recommendations? A systematic review. *PeerJ*, *5*, p.e3093.

Ruiz-Ramos DV, Saunders M, Fisher CR, Baums IB (2015) Home Bodies and Wanderers: Sympatric Lineages of the Deep-Sea Black Coral Leiopathes glaberrima. PLoS ONE 10(10): e0138989. doi:10.1371/journal.pone.0138989

Segurado, P., & Araujo, M. B. (2004). An evaluation of methods for modelling species distributions. *Journal of Biogeography*, *31*(10), 1555-1568.

Shcheglovitova, M. and Anderson, R.P., (2013). Estimating optimal complexity for ecological niche models: a jackknife approach for species with small sample sizes. *Ecological Modelling*, *269*, 9-17.

Tittensor, D.P., Baco, A.R., Brewin, P.E., Clark, M.R., Consalvey, M., Hall-Spencer, J., Rowden, A.A., Schlacher, T., Stocks, K.I. and Rogers, A.D., (2009). Predicting global habitat suitability for stony corals on seamounts. *Journal of Biogeography*, *36*(6), 1111-1128.

Tong, R., Purser, A., Guinan, J., & Unnithan, V. (2013). Modeling the habitat suitability for deep-water gorgonian corals based on terrain variables. *Ecological informatics*, *13*, 123-132.

Tracey, D. M., Rowden, A. A., Mackay, K. A., & Compton, T. (2011). Habitat-forming cold-water corals show affinity for seamounts in the New Zealand region. *Marine Ecology Progress Series*, *430*, 1-22.

Tsoar, A., Allouche, O., Steinitz, O., Rotem, D., & Kadmon, R. (2007). A comparative evaluation of presence-only methods for modelling species distribution. *Diversity and distributions*, *13*(4), 397-405.

Van Der Molen, J., Van Beek, J., Augustine, S., Vansteenbrugge, L., van Walraven, L., Langenberg, V., van der Veer, H.W., Hostens, K., Pitois, S. and

Robbens, J., (2015). Modelling survival and connectivity of Mnemiopsis leidyi in the south-western North Sea and Scheldt estuaries. *Ocean Science*, *11*(3), 405-424.

Villarino, E., Chust, G., Licandro, P., Butenschön, M., Ibaibarriaga, L., Larrañaga, A., & Irigoien, X. (2015). Modelling the future biogeography of North Atlantic zooplankton communities in response to climate change. *Marine Ecology Prog. Ser*, *531*, 121-142.

Waltari, E., & Guralnick, R. P. (2009). Ecological niche modelling of montane mammals in the Great Basin, North America: examining past and present connectivity of species across basins and ranges. *Journal of Biogeography*, *36*(1), 148-161.

Warren, D.L. and Seifert, S.N., (2011). Ecological niche modeling in MAXENT: the importance of model complexity and the performance of model selection criteria. *Ecological Applications*, *21*(2), 335-342.

Williams, G. J., Knapp, I. S., Maragos, J. E., & Davy, S. K. (2010). Modeling patterns of coral bleaching at a remote Central Pacific atoll. *Marine Pollution Bulletin*, *60*(9), 1467-1476.

Yesson, C., Taylor, M.L., Tittensor, D.P., Davies, A.J., Guinotte, J., Baco, A., Black, J., Hall-Spencer, J.M. and Rogers, A.D., (2012). Global habitat suitability of cold-water octocorals. *Journal of Biogeography*, *39*(7), 1278-1292.

Chapter 2

Niche Modelling: A comparison between Modelling Methods best applied for Cnidaria Niche Dispersion Studies

Abstract

Recently, ecological niche modelling has been receiving more attention in several areas in biology, due to the evolution of personal computers, and the increasing availability of data used in modelling. The results obtained can be used in preventive actions such as species management and invasive species distribution. Since its increasing popularity, several algorithms are available and undergoing tests regarding their performance towards different phylum. Marine invertebrates, more specifically cnidarians, present few studies on this field, and should receive closer attention in the next years due to worldwide increases in jellyfish population (blooms), and bleaching in almost every known shallow water coral reef. Because of this gap of information, we chose this still poor studied group to compare three algorithms. We used MAXENT, GARP and AquaMaps in its desktop form and selected them based on other studies comparing algorithms. Our aim was to, based on different organisms of the phylum Cnidaria, *Lychnorhiza lucerna*, *Chrysaora lactea, Phyllorhiza punctata*, *Tamoya haplonema, Ceriantheomorphe brasiliensis* and *Mussismilia hispida,* compare those algorithms and examine which one performed the best. Our results shown that MAXENT outperformed the other algorithms both regarding de Area Under the ROC Curve (AUC) and the map distribution. GARP show varying results with generalized maps and AquaMaps was the least accurate of them. Our results are similar to those found in other papers, thus meaning that MAXENT is the most reliable software when it comes to modelling these animals.

Key words: Cnidaria, Comparison of algorithms, Niche Modelling

1. INTRODUCTION

Ever since World War II, scientific information has been increasingly disseminated. The IBM, in 1953, already used business, industries and science data in mathematical modelling, aiming to predict results minimizing risks and costs (Simon, 1960). Technological concepts are applied to studies such as corporation administration, black hole observation, global resources management, human cells assemblage, DNA manipulation and modelling (Mahoney, 1988).

Computational Modelling has been, through the past years, used and developed in several areas aside from mathematical statistics. In palaeontology, for example, three-dimensional (3-D) modelling allows researchers to obtain important insights in fossils anatomy, development and preservation (Cunningham et al., 2014). It has also been used to study continental shelf dynamics and evolution (Lazure & Jegou, 1998). Among many other scientific approaches, there is the Ecological Niche Modelling (ENM), which has been increasingly used to research matters of ecology, evolution, epidemiology and conservation (Corsi et al., 1999; Peterson & Vieglais, 2001, Welk et al., 2002; Peterson & Shaw, 2003; Elith et al., 2006).

The ecological niche occupied by a species is one of the limiting factors to its distribution, once it presents the limiting conditions to the survival of those individuals (Hutchinson, 1957; Peterson, 2001). The effective niche (observable) is usually smaller than the fundamental niche (theoretical construction) due to anthropic influences and biotic interactions (extinction, competition and geographic barriers) (Burkey, 1995; Peterson et al., 1999a; Pulliam, 2000; Anderson & Martinez-Meyer, 2004).

In order to run the regression analysis, we need data of the organism in its effective niche. Occurrence or biotic data can be obtained through publications, sampling or academic databases (Ponder et al., 2001, Graham et al., 2004; Soberon & Peterson, 2005). Several open access websites provide several global or local distribution data of species, such as Global Biodiversity Information Facility (GBIF) (http://www.gbif.org/), SeaLifeBase (http://www.sealifebase.org/)

and The World Information Network on Biodiversity (REMIB) (http://www.conabio.gob.mx/remib_ingles/doctos/remib_ing.html), (Graham et al., 2004; Pauly et al., 2009).

Due to the increase in modelling applicability, we can find several algorithms with many interface performing differently. Some algorithms like BIOCLIM (Nix, 1986) and DOMAIN (Carpenter et al., 1993) use presence only data, while others like MAXENT (Phillips et al., 2004; 2006), GARP (Stockwell and Peters 1999), ENFA (Hirzel et al., 2002) and GAM (Yee and Mitchell 1991) use presence and some form of absence (or pseudo-absence). Presence data indicate that the species was in the determinate place where the collection happened. The absence is the opposite and that can be considered unreliable data, once it can merely mean that the species still have not arrived at the place or even a researcher error for lack of sampling (Graham et al., 2004). Precise information about a habitat's biodiversity are rather difficult to obtain being either incomplete or containing mainly presence data, especially for marine organisms, where the sampling data is restricted (Peterson, 2001; Anderson et al., 2002).

We chose two popular algorithm and one now so commonly used for comparison. One of the most popular is GARP (Generic Algorithm for Rule-set Production) (Stockwell and Noble, 1991), an integrated special analysis system for predicting distribution of plants and Animals (Stockwell, 1999). The algorithm was developed using sets of rules considering that ecologist often think about patterns in the environment as a rule, but mainly to outperform models that use multivariate techniques. The algorithm has two advantages according to the authors, it is stable under perturbation from data and informative, being complex while using fewer data (Stockwell, 1991). The algorithm most used (of those three) was introduces in 2004, by Phillips et al. They proposed the application of maximum-entropy (MAXENT) techniques in ecological niche modelling. The approach is equivalent to the Gibbs distribution (exponential in a linear combination of features) and it aims to estimate the distribution that is close to uniform of a determinate species, i.e. the maximum entropy. The other algorithm, AquaMaps (Ready et al., 2010) is not so commonly used, but is promising in theory. The authors developed it to predict global ranges exclusively of marine

organisms and compared the algorithm to other four using fish and mammal species.

Several high impact papers have been using niche modelling, such as Martinez-Meyer (2002) that extensively studied several niches of vertebrates, concluding that those similarities of vertebrate clades could be better explained by geographic correlation, rather than phylogeny. Peterson et al (2003) modelled the occupation area for *Hidrilla verticillata*, a North America invasive aquatic plant, thus helping to minimize the potential damage during the invasion. Those predictions have been used for several organisms such as plants, insects, molluscs and various vertebrates (Skov 2000, Hoffmann 2001; Welk et al., 2002; Peterson, 2003).

On marine ecosystems, one of the top planktonic predators are jellyfish (subphylum Medusozoa). These animals can be found in different niches and depths, predating various organisms, mainly fish eggs and crustacean larvae (Purcell, 1985; Nagata et al., 2014). It is a consensus that jellyfish abundance has been increasing in the past few decades in practically all oceans, (Greve, 1994; Graham, 2001; Brodeur et al., 2002; Yan et al., 2004; Christopher et al., 2005; Purcell, 2005; Jiang et al., 2008). They are usually related to anthropic actions, like ballast water (Daskalov et al., 2007), increase in underwater structure (Graham, 2001), overfishing (Purcell, 2001), eutrophication (Malej et al., 2001) and climate change (Purcell et al., 2007, Gibbons & Richardson, 2008). These increases are usually observed close to the coast, affecting the population direct or indirectly by burning tourists or clogging fishing nets affecting the economy (Carpenter, 2004; Owen 2006).

On the other hand, the subphylum Anthozoaria (e.g. corals, sea anemones), we find organisms that suffer the most from the anthropic influences above. Coral reefs are one of the most complex, diverse and productive ecosystems on the planet (Connell, 1978), with a total area of approximately 1,500,000 km^2 (Cooper, 1994). It provides economical resources to coastal cities trough tourism and fishery (Leão et al., 2008), also protecting the coast from natural forces like waves and hurricanes (Mober & Folke, 1999).

In Brazil, the coral *Mussismilia* represents around 70% of Abrolhos reefs structure (Bahia) being this particular reef the largest and richest of the South

Atlantic (Leao & Kikuchi, 2005, Castro et al., 2010). The raise of temperature on the oceans leads to recurring events of zooxanthellae expulsion, and in their absence, reefs lose their capacity to synthesize lipids lower the reabsorption of nitrogen and protein production (Weis & Allemand, 2009, Teece et al., 2011). Throughout history, coral reefs have shown recuperating capacity from climate changes, with a significant example in the Pleistocene with nine episodes of variations of sea levels (Suguio et al., 1985). Nevertheless, none of these changes happened as fast as the ones we have been observing this last decade. It is estimated that until 2030, proximately 60% of the world coral reefs will be lost (Weis & Allamand, 2009).

Still regarding the Anthozoa group, we have the tube anemone *Ceriantheomorphe brasiliensis,* animal with ptychocyst, one type of cnida responsible for building the tube (Daly et al., 2007). The amount of studies with this group is considerably small because of the difficulty in collecting samples (Rosa, 1973); therefore, basic information about the group is still necessary. Stampar et al (2012) presents the only study to date on Ceriantharia biogeography.

Taking in consideration the changes mentioned above, the present study aims to model present and future distribution for six cnidarians in order to compare three modelling algorithms – MAXENT, GARP and AquaMaps- choosing the one that performs best to use in future niche modelling with cnidarians.

2. METHODOLOGY

Our study is based on 830 observation data, collected from database website, divers' photographic documentation and researcher collaboration, for the South Atlantic. The data obtained from website was from the Global Biodiversity Information Facility (http://www.gbif.org/), and contained identification of the year of the sampling and its geographical location. Those data are for four Medusozoa species: *Lychnorhiza lucerna*, *Chrysaora lactea, Phyllorhiza punctata* (Scyphozoa); *Tamoya haplonema* (Cubozoa); and two

Anthozoa species: *Ceriantheomorphe brasiliensis* and *Mussismilia hispida* (Anthozoa).

Environmental data used were obtained from the Bio-Oracle (http://www.oracle.ugent.be/) (Tyberghein et al., 2012), a marine global database exclusive for marine data. Those data are compiled from “Ocean Color Web”, “World Ocean Database 2009” and “Nasa Earth Observations”. We used the “70ºN-70ºS Real Values” for present projections and the scenarios A1B and B1 (described by IPCC representing the UKMO-hadCM3 model) for the 2100 and 2200 models (detailed in http://wwwpcmdi.llnl.gov/ipcc/model_documentation/ipcc_model documentation.php). All variables available in Bio-Oracle were utilized: 1) oceanic temperature (minimum, maximum and mean in ºC), 2) photosynthetic radiation available (mean and maximum), 3) salinity and pH (mean), 4) cloud coverage (minimum, maximum and mean), 5) dissolved oxygen, 6) silicate, 7) nitrate, 8) phosphate and 9) calcite (mean), 10) chlorophyll A (minimum, maximum and mean) and 11) diffuse attenuation (k490) (minimum, maximum and mean) (Tyberghein et al., 2012).

The modelling softwares were MAXENT (version 3.3.3.k) (Phillips & Dudík, 2008), Garp and AquaMaps (version OpenModeller 1.1.0) (de Souza Muñoz et al., 2011). Those algorithms were chosen because of their differences. AquaMaps is the least malleable of the three, with nine layers pre-determined by the algorithm itself, only working with presence and pseudo-absence data, allowing modifications on the OpenModeller data access. MAXENT (maximum entropy) is also based on presence and pseud-absence data (the last one made by the algorithm itself), generating maps that represent the highest probability of the organism distribution (Phillips et al., 2006) and is described in details in Phillips et al. (2004, 2006).

To model with MAXENT, we used data in .csv along with the environmental data from Bio-Oracle. Jackknife was also done and response curves generated. For the OpenModeller modelling the data were in .txt needed by the software, and for the GARP, the same environmental data used in MAXENT were applied. The versions used were Garp-OM with new implementation and AquaMaps-OM beta version. The coordinates in Lat/Long WGS84.

As a result, for every algorithm, there are distribution maps and response curve, so in order to verify their accuracy, we used AUC (the area under the ROC curve), that represents a table of sensitivity (true positive) x specificity (True negative). The values for this curve is 0-1, where 1 indicates the model is accurately representing the niche (Phillips et al., 2006). The average value of 0.5 represent low reliability, which can happen in cases where the model fit the modelling, but the modelling itself if weak (Elith et al., 2006).

Some database, such as FishBase (www.fishbase.org) e SeaLifeBase (www.sealifebase.org) contain predation data form several organisms, including jellyfish. Pauly et al., (2009) show the percentage of organisms consumed by jellyfish. The same paper presents a low number of jellyfish predators, not enough to cause significant impact on the group. For these reason, we did not consider those data for the present paper, simplifying the problem, resulting in less noise from the models.

3. RESULTS

3.1 General algorithm analysis

The lowest AUC value observed is for AquaMaps, 0.87 for *C. lactea*. GARP's lowest is 0.88 for *L. lucerna*'s 2200 distribution on GARP, and Maxent's lowest value is 0.907 for the 2200 distribution for *T. haplonema* (table 1). Higher values of 0.999 are observed both for GARP and MAXENT. With the exeption of *Mussismilia hispida's* present distribution with GARP algorithm, all present AUCs were higher than or equal to AUCs for future distributions.

AUC's above 0.99 represent 44.4% of Maxent's values, and on 62.5% of those cases, the values are observed on present distributions. GARP presents similar results, with 50% of the highest values corresponding to present distributions. There are only 6 times where the Maxent's AUC are inferior to GARP's and most of them on future distributions, with the exception for *T. haplonema*. As for AquaMaps values, only for *T. haplonema* and *M. hispida* those

values are higher than MAXENT's or GARP's, but when it is higher than GARP's, it is equal to or lower than MAXENT's, and vice versa (table 1).

The AUC average values for present distributions vary according to the species, but is clearly more consistent on MAXENT, followed by GARP and AquaMaps presenting lower values. Future distributions exhibit similar results, with Maxent outperforming GARP by 0.006 (table 2-3). The differences observed between MAXENT and GARP's AUC can be biologically significant and observable on the maps of distribution. These maps, most of the times, represent a different distribution due to different digits on the second or third decimal place.

Table 1│ *Lychnorhiza lucerna*, *Chrysaora lactea, Phyllorhiza punctata*, *Tamoya haplonema, Ceriantheomorphe brasiliensis* and *Mussismilia hispida,* individual AUC value for present distribution models for GARP, MAXENT and AquaMaps. Individual AUC values for future distribution models (2100 and 2200) for MAXENT and GARP.

	YEAR	AUC GARP	AUC MAXENT	AUC AQUAMAPS
Lychnorhiza lucerna	2016	0,98	0,998	0,96
	2100	0,91	0,987	-
	2200	0,88	0,996	-
Chrysaora lactea	2016	0,98	0,997	0,87
	2100	0,97	0,922	-
	2200	0,93	0,952	-
Phyllorhiza punctata	2016	0,99	0,992	0,97
	2100	0,98	0,954	-
	2200	0,93	0,955	-
Tamoya haplonema	2016	0,999	0,978	0,99
	2100	0,98	0,939	-
	2200	0,99	0,907	-
Ceriantheomorphe brasiliensis	2016	0,999	0,999	0,98
	2100	0,999	0,998	-
	2200	0,98	0,998	-
Mussismilia hispida	2016	0,91	0,999	0,98
	2100	0,99	0,979	-
	2200	0,96	0,985	-

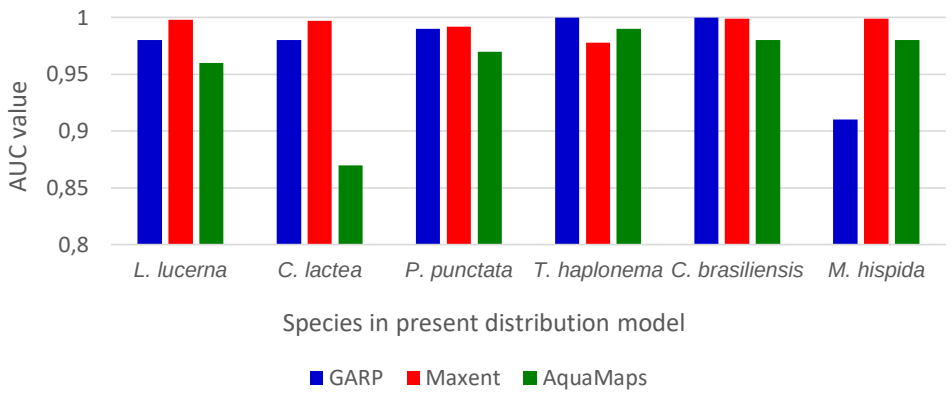

Figure 1| AUC accuracy for present models for *Ceriantheomorphe brasiliensis, Mussismilia hispida* (Anthozoa), *Tamoya haplonema*, *Phyllorhiza punctata, Chrysaora lactea* and *Lychnorhiza lucerna* (Medusozoa). Green is AquaMaps, red is MAXENT and blue GARP

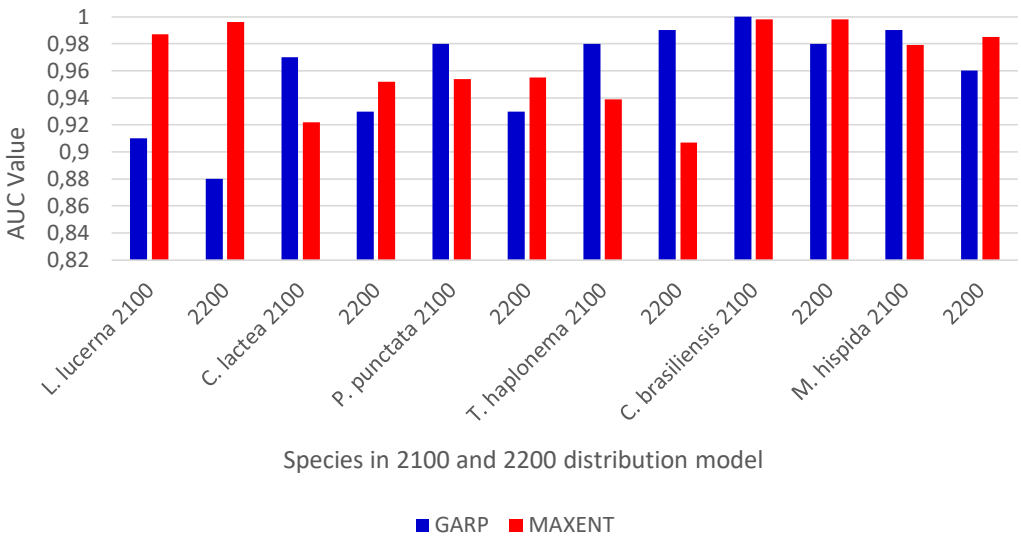

Figure 2| AUC values for each species for future models (2100 and 2200), for *Ceriantheomorphe brasiliensis, Mussismilia hispida* (Anthozoa), *Tamoya haplonema*, *Phyllorhiza punctata, Chrysaora lactea* and *Lychnorhiza lucerna* (Medusozoa). Red is MAXENT plots and blue, GARP.

Table 2│ Present distribution average AUCs for the three algorithms – GARP, MAXENT, AquaMaps. The values here presented are the sum of the species AUCs and divided by the count of that series of number.

Average AUC Values for Present Distribution			
Algorithm	GARP	MAXENT	AquaMaps
Average Value	0,976	0,993	0,958

Table 3│Average for future distribution AUC for GARP and MAXENT. The values are the sum of the species values and divided by the count of that series of number.

Average AUC Values for Future Distribution		
Algorithm	GARP	MAXENT
Average Value	0,958	0,964

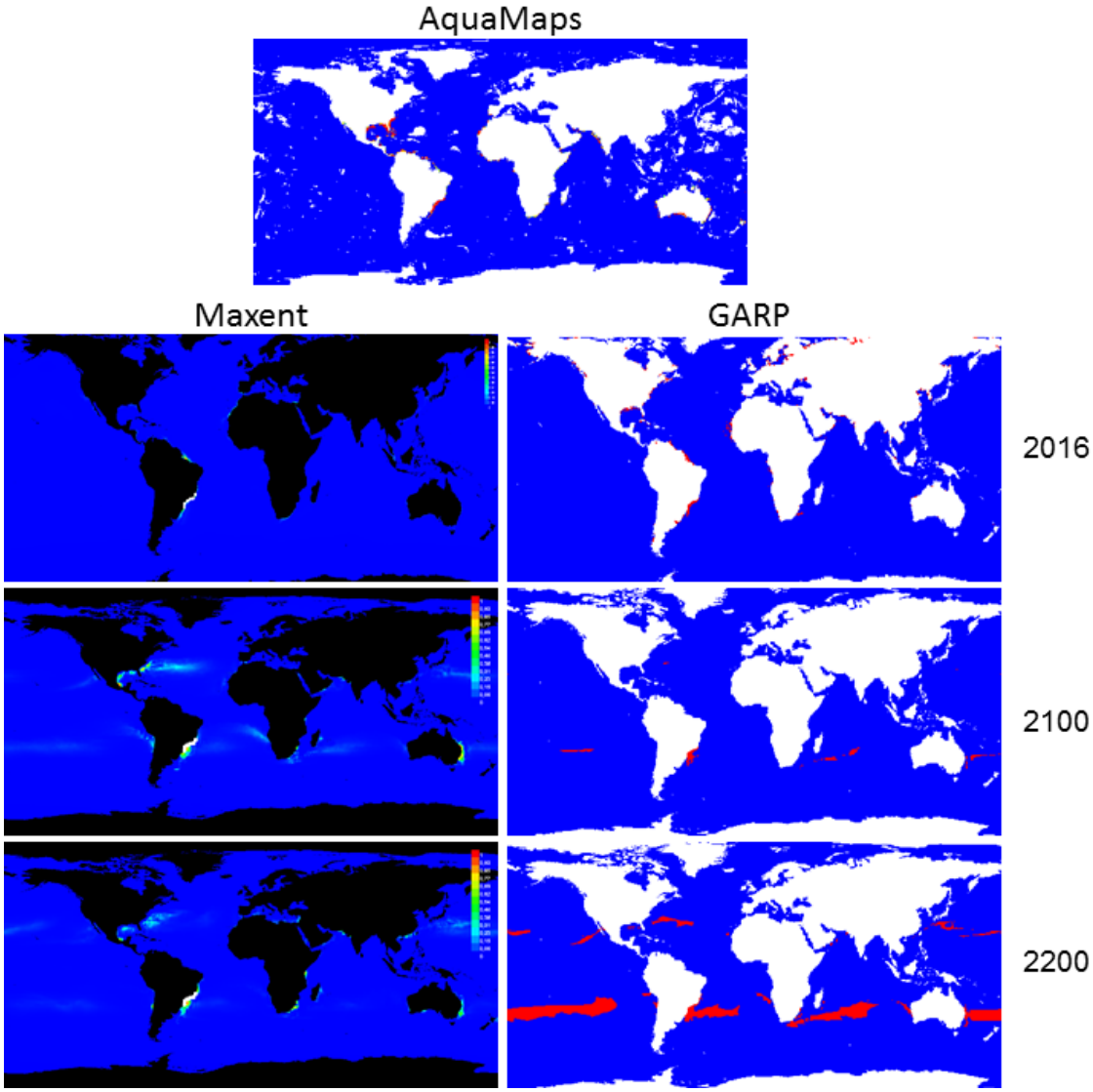

Figure 3| AquaMaps, MAXENT and GARP distribution maps for *Ceriantheomorphe brasiliensis.* The first maps represent the present distribution, followed by the 2110 and 2200 distribution respectively for MAXENT and GARP.

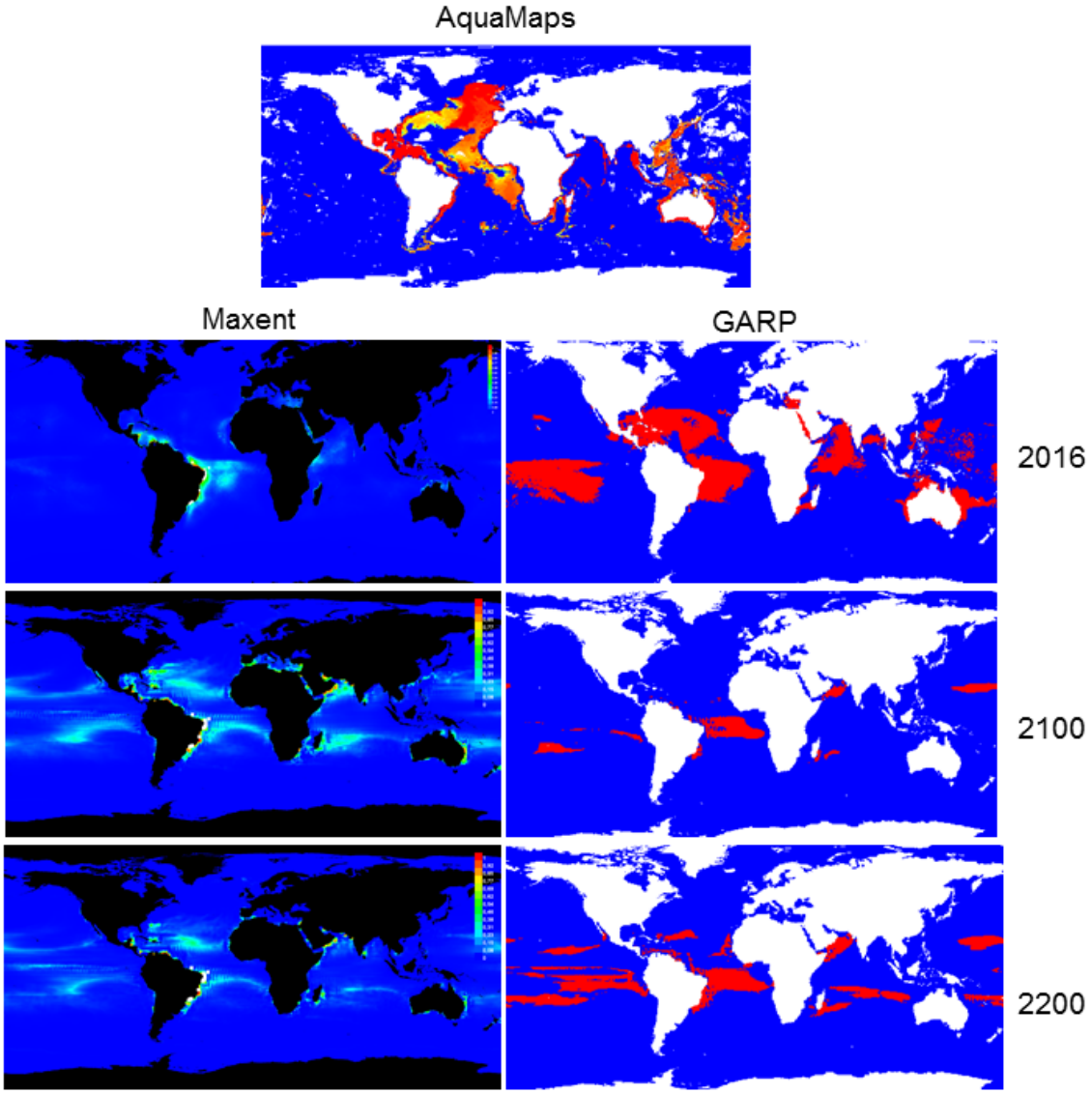

Figure 4│ AquaMaps, MAXENT and GARP distribution maps for *Mussismilia hispida.* The first maps represent the present distribution, followed by the 2110 and 2200 distribution respectively for MAXENT and GARP. AquaMaps only presents one map of present distribution due to its predefined layers.

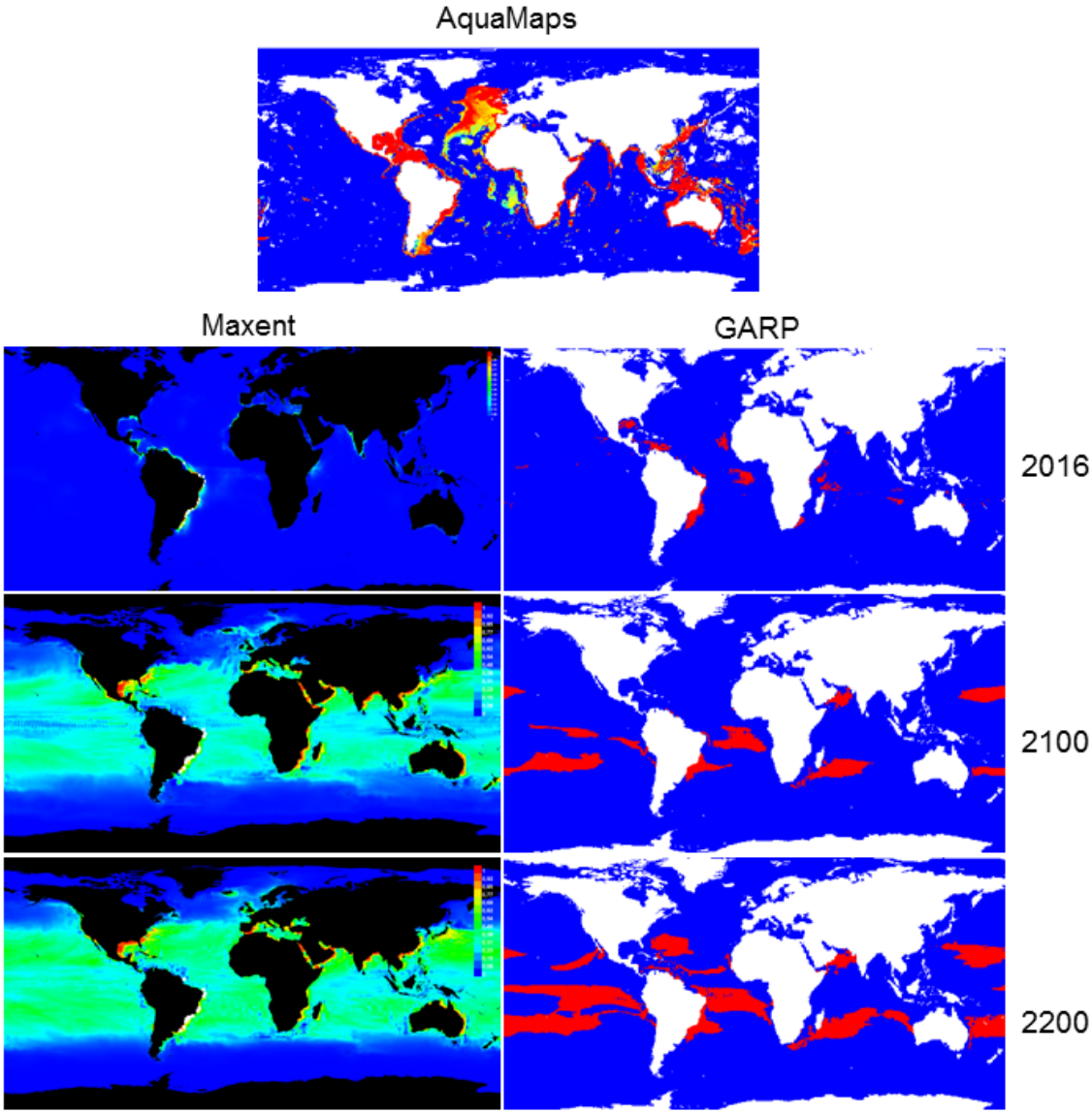

Figure 5│ AquaMaps, MAXENT and GARP distribution maps for *Chrysaora lactea.* The first maps represent the present distribution, followed by the 2110 and 2200 distribution respectively for MAXENT and GARP.

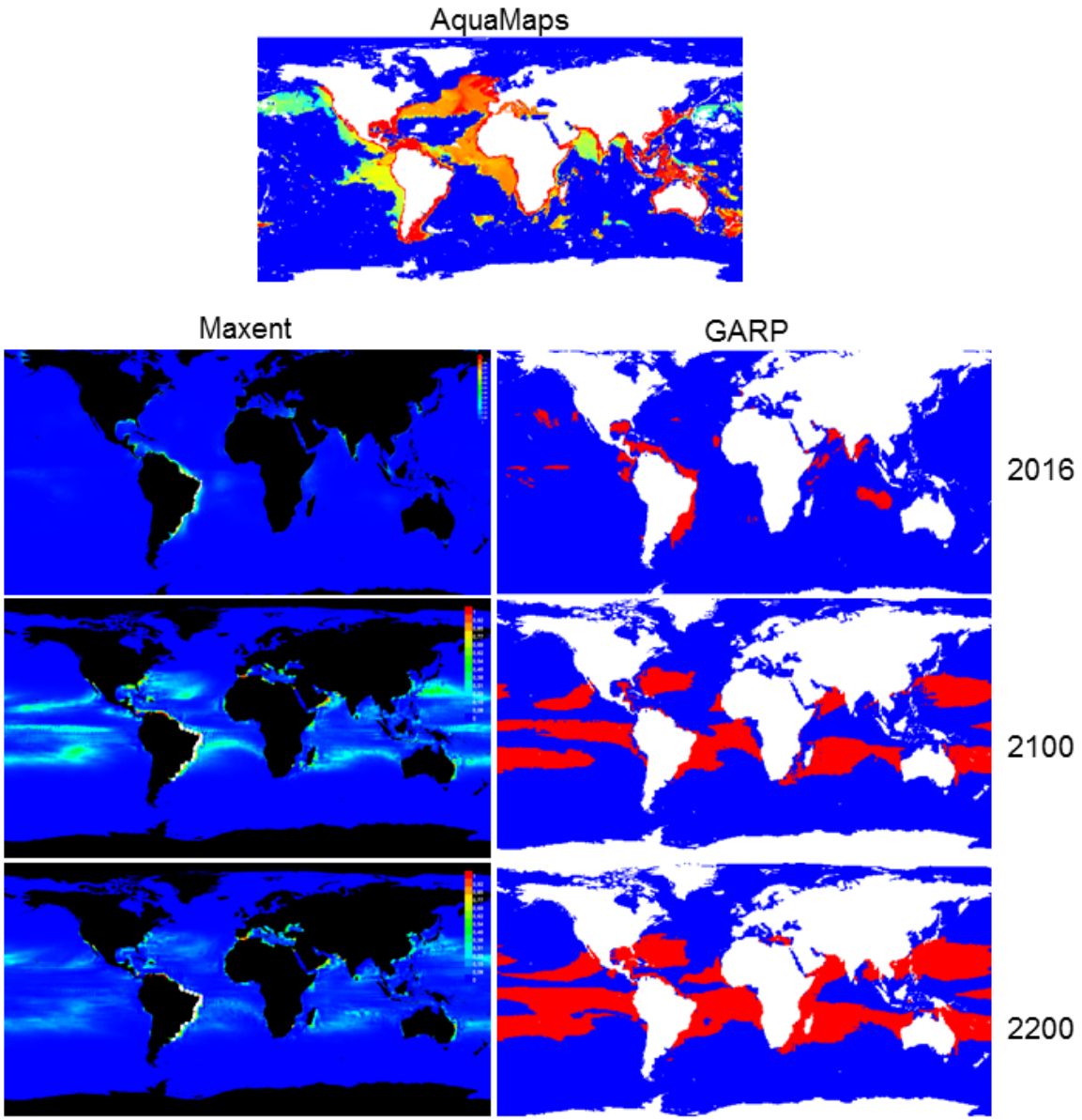

Figure 6│ AquaMaps, MAXENT and GARP distribution maps for *Lychnorhiza lucerna.* The first maps represent the present distribution, followed by the 2110 and 2200 distribution respectively for MAXENT and GARP.

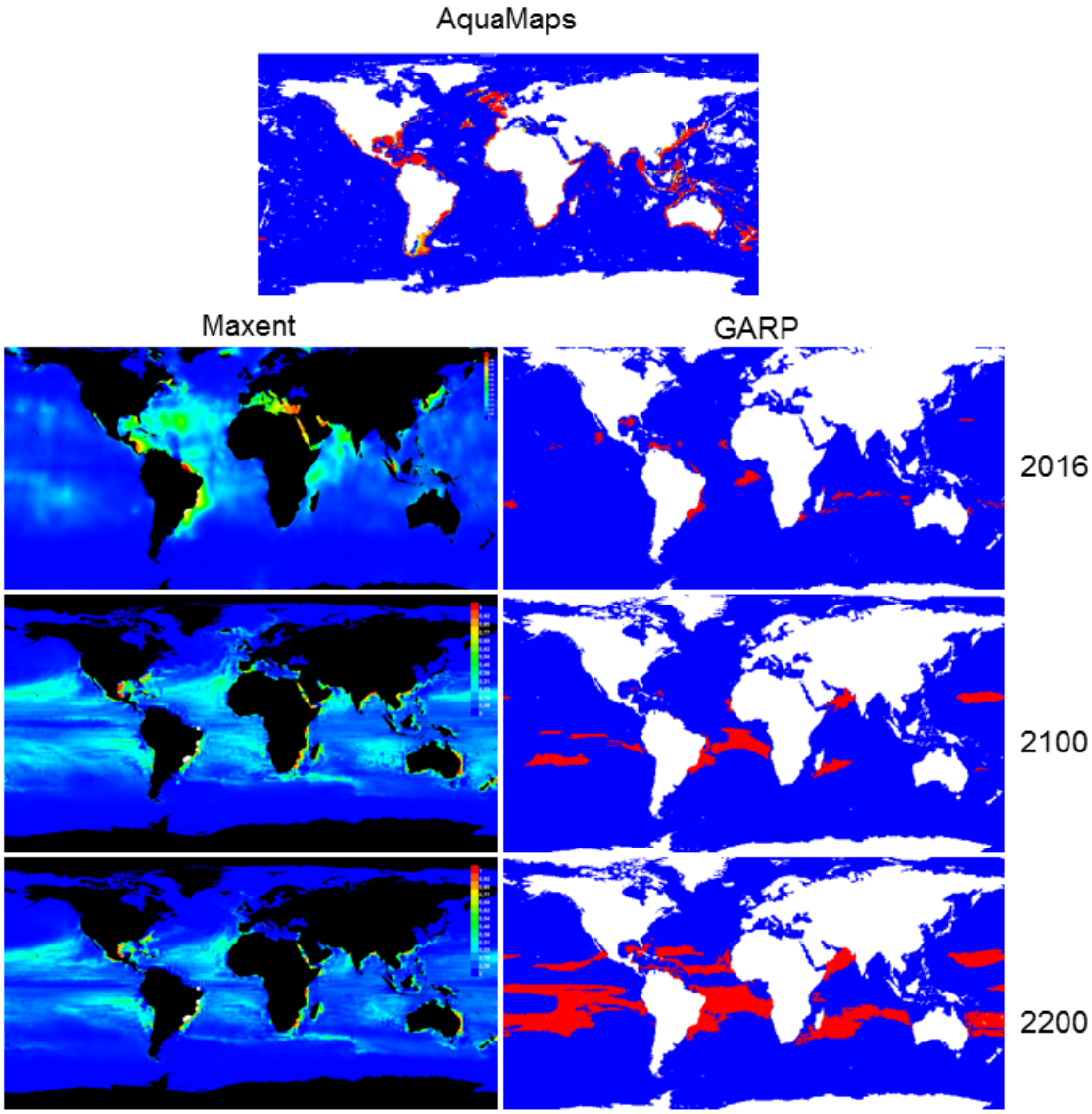

Figure 7│ AquaMaps, MAXENT and GARP distribution maps for *Phyllorhiza punctata.* The first maps represent the present distribution, followed by the 2110 and 2200 distribution respectively for MAXENT and GARP.

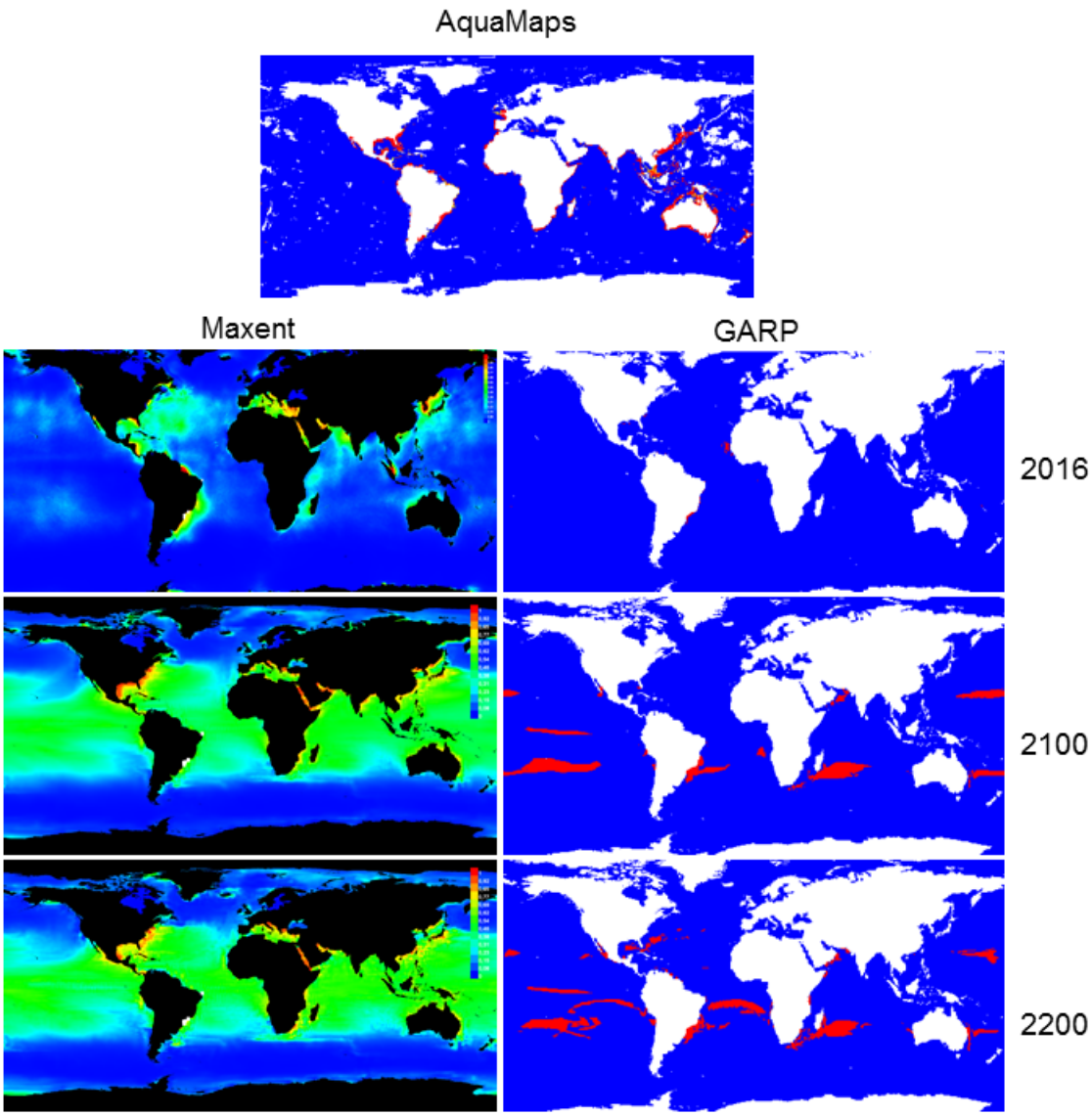

Figure 8│ AquaMaps, MAXENT and GARP distribution maps for *Tamoya haplonema.* The first maps represent the present distribution, followed by the 2110 and 2200 distribution respectively for MAXENT and GARP.

3.2 Ceriantheomorphe brasiliensis

AquaMaps only presents one map of present distribution due to its predefined layers. MAXENT present map represents what we know, so far, to be the distribution of this species' habitats, and future niche probability seems acceptable, with environments mostly in shallow water. GARP present map shows more probable habitats than what is currently known for these organisms. Future distributions for this algorithm is slightly more generalized, presenting possible habitats on, theoretically, deeper waters. AquaMaps' points of distribution are mostly different from the other two algorithms, even though it is contained in coastal areas, some places shown by the map are not know to have the present specie

3.3 Mussismilia hispida

AquaMaps only presents one map of present distribution due to its predefined layers. Maxent present map is an expected distribution, with most probable habitats close to the coast, on shallower water. Map for 2100 plot the distribution beyond Brazil, with several continents' coastal zones habitats possible for occupation. The 2200, map for this algorithm shows a decrease on this areas compared to the century before. GARP present map is much more generalized, with possible presence points in deep parts of the ocean, and several continents where these animals have not been found so far. Future distribution for 2100 shows a decrease of this possible habitats, and a slight increase for 2200.

3.4 Chrysaora lactea

AquaMaps only presents one map of present distribution due to its predefined layers. Maxent map of distribution contain what we know, so far about this organism's distribution, with only one point in the Indian Ocean not yet known. Future distribution for this algorithm show an increase for the year 2100 and a

decrease in some places for 2200, but all the most likely points are close to shore, where this animals would be expected to be found. GARP present maps are relatively close to the Maxent one, with only a few extra points far from shore. Future maps distribution show an increase from 2100 and 2200 and possible habitats points are not contained in the coastal areas. AquaMaps is the most generalized map with different areas of distribution than the ones currently found for the *C. lactea*.

3.5 Lychnorhiza lucerna

AquaMaps only presents one map of present distribution due to its predefined layers. Maxent present distribution map represent the currently know distribution for this Brazilian endemic species, with a low probability of presence on Indian Ocean. For 2100, there is an increase in this organism's possible habitat, with a slight decrease in 2200, and high spots probability always close to coastal zones. GARP present and future distributions show highly generalized maps with increases for the future and possible habitats on almost every continent. AquaMaps present distribution is even more generalized than GARP's with probable presence in countries where these animals are not currently found.

3.6 Phyllorhiza punctata

AquaMaps, Maxent and GARP distribution maps for *Phyllorhiza punctata.* The first maps represent the present distribution, followed by the 2110 and 2200 distribution respectively for Maxent and GARP. AquaMaps only presents one map of present distribution due to its predefined layers. Maxent present map show a more generalized result than expected, even though presence is more likely on costal zones, where the specie is usually found. Future distribution is more contained to costal zones rather than oceanic spots, which is most likely to happen. GARP show a consistence increase for the year 2100 and 2200 of places where this organism can inhabit. Present distribution map closely represent expected habitats for *P. punctata.* AquaMaps map show a global

distribution, tending close to the coast of the countries, where the specie is plotted to be.

3.7 Tamoya haplonema

AquaMaps only presents one map of present distribution due to its predefined layers. Maxent shows, though colour differentiation, that coastal zones present a higher probability of dispersion on that niche; while cold colour green represents a less probable, but still possible niche for this species distribution. GARP maps show a more contained distribution for the present and future for this species. AquaMaps distribution is also contained and closer to continental waters.

4. DISCUSSION

There is not a consensus on the amount of data necessary in order to obtain a good response from the model. Our results have presented Maxent's highest AUC numbers and best performances from *Ceriantheomorphe brasiliensis* and Lychnorhiza lucerna, species with higher presence points. Nevertheless, GARP's best projections were on *Tamoya haplonema, Phyllorhiza punctata and Ceriantheomorphe brasiliensis,* with amount of data differing, with the first too presenting fewer information.

Several studies that intended to compare a range of modelling algorithms show MAXENT outperforming GARP (Elith et al., 2006, Phillips et al., 2006, Peterson et al., 2007; Bentlage et al., 2009). Our results have shown that MAXENT is the most suitable algorithm with higher AUC values, result also found on and corroborated by the articles mentioned above. However, Ready et al. (2010) compared AquaMaps, Garp and MAXENT for marine mammals and fish and according to their results, AquaMaps outperformed GARP and equalled MAXENT. Our results were different, with AquaMaps being the least reliable of all three. The fact that the algorithm allows only pre-determined environmental

data, can affect the accuracy when compared to other algorithms, since the data used on those layers, are, mostly, from the 90's and the data used in the Bio-Oracle are real time.

Our analysis have shown that MAXENT maps for the present, represent a close dispersion observed for these organisms by Morandini et al (2005)**,** while the maps presented by GARP represent a more general dispersion in practically all models. Since it does not have colour distinction for occupational probability, it tends to overestimate favourable occupational habitats, with unlikely niches for the species on present and future distribution, especially when considering the benthic animals. AquaMaps is an algorithm still rarely used, and comparing it with the other models, it lacks precision in most analysis with both maps distribution plots and AUC values. It is clear that even small differences between MAXENT and GARP's AUC, they can be biologically significant. With our maps, it is possible to notice that slight alteration on the AUC values can change dispersion of the organisms in the distribution maps.

The amount of data necessary for an algorithm is still uncertain. Our MAXENT results show that the amount of data used by the model is directly proportional to the reliability. More presence data means better model output, and higher the AUC values, which is observed on the *Ceriantheomorphe brasiliensis* and *Lychnorhiza lucerna* plots. *Phyllorhiza punctata* and *Tamoya haplonema* have lower observation data thus resulting in slightly lower AUCs. On the other hand, Garp presented the highest AUCs for *T. haplonema, P. punctata* and *C. brasiliensis*, and lower for *M. hispida* and *C. lactea* (future model). This is evidence that this particular algorithm is not restricted to amount of observation data, but is rather affected by the reliability of data, also observed in the extensive work of Elith et al. (2006). It is safe to assumethat the amount of occurrence data influences the optimization and reliability of the model. There is not, so far, a pattern for all of them, and in literature, we can observe divergence in standardizing of the necessary occurrence data to reach maximum accuracy for a species (Stockwell & Peterson, 2002; Elith et al., 2006; Bentlage et al., 2009; Peterson & Vieglais, 2001).

Despite the range of applicability for species distribution model, the greatest challenge in marine ecosystems, is integrating models from different

trophic level considering that general habits are still little understood. A solution can be simplifying the problem, so that richness parameters and biological relevance are related (de Young et al., 2004). Merrow et al., (2014) highlights that statement, indicating that choosing complex models, with several different taxa can result in a challenge when comparing complexity and noise.

Another potential problem in species distribution modelling is the commonly employed assumption that niches are stable though time, especially regarding invasive species and responses to climate change (Martines-Meyer et al., 2004; Pearman et al., 2008). Ecological niche modelling analyses tend to assume that physical expression of a realized niche of a taxon depends upon the interactions of several factors, including biotic, abiotic and migration limitations (Peterson et al., 2011). Under this paradigm, any change in environmental and geological variables should result in a change in geographic space. However, this relationship is complex, with geographic distribution being bi-dimensional, while ecological niches are multidimensional, where *N* dimensions equals the number of variables defining them (Peterson et al., 2011). In order to verify if biotic and abiotic changes should be taken into consideration due to stability on niche models, Brame & Stigall (2014) modelled the niche stability through geological time. They used paleontological data from invertebrates from the late Ordovician, with MAXENT and GARP. The results showed the niche was highly stable during intervals characterized by gradual abiotic environmental change. They concluded that the niche stability is valid under climate change or any other gradual abiotic environmental change. Conversely to it, when under intervals of biotic changes, species invasion or intraspecific variability, niches were less stable and such changes should be taken into consideration while modelling this scenario (Wisz et al., 2013; Chust et al., 2017)

5. CONCLUSION

Considering the sessile and vagile animals here presented, the best algorithm to model their distribution is MAXENT, presenting both high AUC values and close to reality maps. Nonetheless, despite differences between the

algorithms, on every distribution map for the year 2200 there is a decrease in all possible habitats.

In general, the ocean's circulation is a limiting factor for geographic distribution for marine species (Chavez et al., 2003), and any change in the physicochemical structure we find now can affect the organisms' growth and survival, as much as larval distribution and competition through the entire oceanic chain. Presently, the most detailed models are those in which the organism in question is in higher trophic levels probably because of their increased knowledge. However, even though the amount of information is greater, the model itself is incomplete, lacking details from basal organisms (de Young et al., 2004). It is important to stress that through niche modelling, we are able to answer questions that would otherwise be difficult to answer (Bentlage et al., 2009), although there is no computational model, to date, to simulate all the possible ecosystems in every ocean. It is also important to highlight the need of more research in these areas, both on cnidarians habits, and modelling algorithms, in order to make the tool even more precise than it already is. Moreover, we are not claiming our results as a definitive pattern, especially for future models, but presenting a possible and yet changeable scenario.

6. REFERENCES

Anderson, R. P., & Martınez-Meyer, E. (2004). Modeling species' geographic distributions for preliminary conservation assessments: an implementation with the spiny pocket mice (*Heteromys*) of Ecuador. *Biological Conservation*, *116*, 167–179.

Anderson, R.P., Peterson, A.T., Gómez-Laverde, M., (2002). Using niche-based GIS modeling to test geographic predictions of competitive exclusion and competitive release in South American pocket mice. Oikos 98, pp.3–16

Bahn, V., & McGill, B. J. (2007). Can niche-based distribution models outperform spatial interpolation? *Global Ecology and Biogeography*, *16*(6), 733-742.

Bentlage, B., Cartwright, P., Yanagihara, A. A., Lewis, C., Richards, G. S., & Collins, A. G. (2009). Evolution of box jellyfish (Cnidaria: Cubozoa), a group of highly toxic invertebrates. *Proceedings of the Royal Society of London B: Biological Sciences*, rspb20091707.

Brame, H. M. R., & Stigall, A. L. (2014). Controls on niche stability in geologic time: congruent responses to biotic and abiotic environmental changes among Cincinnatian (Late Ordovician) marine invertebrates. *Paleobiology*, *40*(1), 70-90.

Brodeur, R. D., Sugisaki, H., & Hunt, G. L. (2002). Increases in jellyfish biomass in the Bering Sea: implications for the ecosystem. *Marine Ecology Progress Series*, *233*.

Burkey T V. (1995). Extinction rates in archipelagoes: implications for populations in fragmented habitats. *Conservation Biology* 9, 527–541.

Carpenter, G., Gillison, A. N., & Winter, J. (1993). DOMAIN: a flexible modelling procedure for mapping potential distributions of plants and animals. *Biodiversity and conservation*, *2*(6), 667-680.

Chavez, F. P., Ryan, J., Lluch-Cota, S. E., & Ñiquen, M. (2003). From anchovies to sardines and back: multidecadal change in the Pacific Ocean. *Science*, *299*(5604), 217-221.

Lynam, C. P., Hay, S. J., & Brierley, A. S. (2005). Jellyfish abundance and climatic variation: contrasting responses in oceanographically distinct regions of the North Sea, and possible implications for fisheries. *Journal of the Marine Biological Association of the United Kingdom*, *85*(03), 435-450.

Chust, G., Vogt, M., Benedetti, F., Nakov, T., Villéger, S., Aubert, A., ... & Bittner, L. (2017). Mare incognitum: A glimpse into future plankton diversity and ecology research. *Frontiers in Marine Science*, *4*(122).

Connell, J.H. (1978). Diversity in tropical rain forest and coral reef. Science 199(4335) 1302-1310.

Copper, P. (1994). Ancient reef ecosystem expansion and collapse. *Coral reefs*, *13*(1), 3-11.

Corsi, F., Dupre, E., Boitani, L., (1999). A large-scale model of wolf distribution in Italy for conservation planning. Conservation Biology 13, 150–159.

Cunningham, J. A., Rahman, I. A., Lautenschlager, S., Rayfield, E. J., & Donoghue, P. C. (2014). A virtual world of paleontology. *Trends in ecology & evolution*, *29*(6), 347-357.

Daly, M., Brugler, M. R., Cartwright, P., Collins, A. G., Dawson, M. N., Fautin, D. G., France, S.C., McFadden, C.S., Opresko, D.M., Rodriguez, E. and Romano, S.L.,& Romano, S. L. (2007). The phylum Cnidaria: a review of phylogenetic patterns and diversity 300 years after Linnaeus.

Daskalov, G.M., Grishin, A.N., Rodionov, S. and Mihneva, V., (2007). Trophic cascades triggered by overfishing reveal possible mechanisms of ecosystem regime shifts. *Proceedings of the National Academy of Sciences*, *104*(25), 10518-10523.

de Souza Muñoz, M.E., De Giovanni, R., de Siqueira, M.F., Sutton, T., Brewer, P., Pereira, R.S., Canhos, D.A.L. and Canhos, V.P., (2011). openModeller: a generic approach to species' potential distribution modelling. *GeoInformatica*, *15*(1), 111-135.

De Young, Heath, M., Werner, F., Chai, F., Megrey, B., & Monfray, P. (2004). Challenges of modeling ocean basin ecosystems. *Science*, *304*(5676), 1463-1466.

Castro, A. P., Arau´ jo, S. D., Jr, Reis, A. M., Moura, R. L., Francini- Filho, R. B., Pappas, G., Jr, Rodrigues, T. B., Thompson, F. L. & Krü ger, R. H. (2010). Bacterial community associated with healthy and diseased reef coral *Mussismilia hispida* from eastern Brazil. Microb Ecol 59, 658–667.

Elith, J. P Anderson, R., Dudík, M., Ferrier, S., Guisan, A., J Hijmans, R., Huettmann, F., R Leathwick, J., Lehmann, A., Li, J., G Lohmann, L. and A Loiselle, B., (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, *29*(2), 129-151

Gibbons, M.J. and Richardson, A.J. (2008). Patterns of pelagic cnidarian abundance in the North Atlantic. Hydrobiologia 616, 51–65

Graham, C. H., Ferrier, S., Huettman, F., Moritz, C., & Peterson, A. T. (2004). New developments in museum-based informatics and applications in biodiversity analysis. *Trends in ecology & evolution*, *19*(9), 497-503.

Graham, W.M., (2001). Numerical increases and distributional shifts of *Chrysaora quinquecirrha* (Desor) and *Aurelia aurita* (Linne) (Cnidaria: Scyphozoa) in the northern Gulf of Mexico. Hydrobiologia 451, 97– 111.

Greve, W. (1994). The 1989 german bight invasion of muggiaea atlantica. *ICES Journal of Marine Science: Journal du Conseil*, *51*(4), 355-358.

Hirzel, A. H., Hausser, J., Chessel, D., & Perrin, N. (2002). Ecological-niche factor analysis: how to compute habitat-suitability maps without absence data?. *Ecology*, *83*(7), 2027-2036.

Hoffmann, M. H. (2001). The distribution of Senecio vulgaris: capacity of climatic range models for predicting adventitious ranges. *Flora*, *196*(5), 395-403.

Hutchinson, G. E. (1957). Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, *22* pp.415–427.

Jiang, H., Cheng, H.Q., Xu, H.G., Arreguín-Sánchez, F., Zetina-Rejón, M.J., Luna, P.D.M. and Le Quesne, W.J., (2008). Trophic controls of jellyfish blooms and links with fisheries in the East China Sea. *Ecological Modelling*, *212*(3), 492-503.

Kearney, M., & Porter, W. (2009). Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology letters*, *12*(4), 334-350.

Lazure, P., & Jégou, A. M. (1998). 3D modelling of seasonal evolution of Loire and Gironde plumes on Biscay Bay continental shelf. *Oceanologica acta*, *21*(2), 165-177.

Leão, Z. M., & Kikuchi, R. K. (2005). A relic coral fauna threatened by global changes and human activities, Eastern Brazil. *Marine Pollution Bulletin*, *51*(5), 599-611.

Leão, Z. M., Kikuchi, R.K.P.D., & Oliveira, M.D.D.M.D. (2008). Branqueamento de corais nos recifes da Bahia e sua relação com eventos de

anomalias térmicas nas águas superficiais do oceano. *Biota Neotropica*, *8*(3), 69-82.

Libralato, S., Christensen, V., & Pauly, D. (2006). A method for identifying keystone species in food web models. *ecological modelling*, *195*(3), 153-171.

Mahoney, M. S. (1988). The history of computing in the history of technology. *Annals of the History of Computing*, *10*(2), 113-125.

Malej, A. (2001). Are irregular plankton phenomena getting more frequent in the northern Adriatic Sea. In *Gelatinous zooplankton outbreaks: theory and practice. CIESM Workshop Series, Monaco* ,14, 67-68.

Martınez-Meyer, E., A. T. Peterson, and W. W. Hargrove. (2004). Ecological niches as stable distributional constraints on mammal species, with implications for Pleistocene extinctions and climate change projections for biodiversity. Global Ecology and Biogeography 13 305–314.

Martínez-Meyer, E., 2002. Evolutionary trends in ecological niches of species. Unpublished PhD Dissertation, Department of Geography, University of Kansas, Lawrence, Kansas.

Merow, C., Smith, M.J., Edwards, T.C., Guisan, A., McMahon, S.M., Normand, S., Thuiller, W., Wüest, R.O., Zimmermann, N.E. and Elith, J. (2014). What do we gain from simplicity versus complexity in species distribution models? *Ecography*, *37*(12), 1267-1281.

Moberg, F., & Folke, C. (1999). Ecological goods and services of coral reef ecosystems. *Ecological economics*, *29*(2), 215-233.

Morandini, A. C., Ascher, D., Stampar, S. N., & Ferreira, J. F. V. (2005). Cubozoa e Scyphozoa (Cnidaria: Medusozoa) de águas costeiras do Brasil. *Iheringia, Série Zoologia*, *95*(3) 281-294

Nagata, R. M., Júnior, M. N., Brandini, F. P., & Haddad, M. A. (2014). Spatial and temporal variation of planktonic cnidarian density in subtropical waters of the Southern Brazilian Bight. *Journal of the Marine Biological Association of the United Kingdom*, *94*(07), 1387-1400.

Nix, H. A. (1986). A biogeographic analysis of Australian elapid snakes. *Atlas of elapid snakes of Australia*, *7*, 4-15.

Pauly, D., Graham, W., Libralato, S., Morissette, L., & Palomares, M. D. (2009). Jellyfish in ecosystems, online databases, and ecosystem models. *Hydrobiologia*, *616*(1) 67-85.

Pearman, P. B., Randin, C. F., Broennimann, O., Vittoz, P., Knaap, W. O., Engler, R., & Guisan, A. (2008). Prediction of plant species distributions across six millennia. *Ecology Letters*, *11*(4), 357-369.

Peterson, A. T., & Vieglais, D. A. (2001). Predicting Species Invasions Using Ecological Niche Modeling: New Approaches from Bioinformatics Attack a Pressing Problem: A new approach to ecological niche modeling, based on new tools drawn from biodiversity informatics, is applied to the challenge of predicting potential species' invasions. *BioScience*, *51*(5), 363-371.

Peterson, A. T. (2001). Predicting Species' Geographic Distributions Based on Ecological Niche Modeling. *The Condor*, *103*(3) 599-605.

Peterson, A. T. (2003). Predicting the geography of species' invasions via ecological niche modeling. *The quarterly review of biology*, *78*(4) 419-433.

Peterson, A. T., Papes, M., & Kluza, D. A. (2003). Predicting the potential invasive distributions of four alien plant species in North America. *Weed Science*, *51*(6) 863-868.

Peterson, T A., Papeş, M., & Eaton, M. (2007). Transferability and model evaluation in ecological niche modeling: a comparison of GARP and MAXENT. *Ecography*, *30*(4) 550-560.

Peterson, A. T., J. Soberon, R. G. Pearson, R. P. Anderson, E. Martınez-Meyer, M. Nakamura, and M. B. Araujo. (2011). Ecological niches and geographic distributions. Princeton University Press, Princeton.

Ready, J., Kaschner, K., South, A. B., Eastwood, P. D., Rees, T., Rius, J. & Froese, R. (2010). Predicting the distributions of marine organisms at the global scale. *Ecological Modelling*, *221*(3), 467-478.

Peterson, A. T., J. Soberon, V. Sanchez-Cordero. (1999). Conservatism of ecological niches in evolutionary time. Science 285, 1265–1267.

Peterson, A.T., Cohoon, K.P., (1999). Sensitivity of distributional prediction algorithms to geographic data completeness. Ecol. Model. 117, 154–164.

Peterson, A. T., & Shaw, J. (2003). Lutzomyia vectors for cutaneous leishmaniasis in Southern Brazil: ecological niche models, predicted geographic distributions, and climate change effects. *International journal for parasitology*, *33*(9), 919-931.

Phillips, S. J., Dudík, M., & Schapire, R. E. (2004, July). A maximum entropy approach to species distribution modeling. In *Proceedings of the twenty-first international conference on Machine learning* (p. 83). ACM.

Phillips, S. J., & Dudík, M. (2008). Modeling of species distributions with MAXENT: new extensions and a comprehensive evaluation. *Ecography*, *31*(2), 161-175.

Phillips, S.J., R.P. Anderson & R.E. Schapire. (2006). Maximum entropy modeling of species geographic distributions. Ecological Modelling 190, 231-259.

Ponder, W. F., Carter, G. A., Flemons, P., & Chapman, R. R. (2001). Evaluation of museum collection data for use in biodiversity assessment. *Conservation biology*, *15*(3), 648-657.

Pulliam, H. R. (2000). On the relationship between niche and distribution. *Ecology letters*, *3*(4), 349-361.

Purcell, J.E. (1985). Predation on fish eggs and larvae by pelagic cnidarians and ctenophores. Bulletin of Marine Science 37, 739–755

Purcell, J. E. (2005). Climate effects on formation of jellyfish and ctenophore blooms: a review. *Journal of the Marine Biological Association of the United Kingdom*, *85*(03), 461-476.

Purcell, J.E. and Arai, M.N. (2001) Interactions of pelagic cnidarians and ctenophores with fish: a review. Hydrobiologia 451, 27–44

Purcell, J. E., Uye, S. I., & Lo, W. T. (2007). Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. *Marine Ecology Progress Series*, *350*, 153-174.

Ready, J., Kaschner, K., South, A. B., Eastwood, P. D., Rees, T., Rius, J., ... & Froese, R. (2010). Predicting the distributions of marine organisms at the global scale. *Ecological Modelling*, *221*(3), 467-478.

Remondino, F., & El-Hakim, S. (2006). Image-based 3D modelling: A review. *The Photogrammetric Record*, *21*(115), 269-291.

Rosa, C.N. (1973). Os animais de nossas praias (2 ed.). São Paulo: Edart

Simon, Herbert A. (1960). The New Science of Management Decision. New York, Harper & Row.

Skov, F. (2000). Potential plant distribution mapping based on climatic similarity. *Taxon*, 503-515.

Soberon, J., & Peterson, A. T. (2005). Interpretation of models of fundamental ecological niches and species' distributional areas.

Stampar SN, Maronna MM, Morandini AC et al (2012) Evolutionary diversifi cation of banded tube-dwelling anemones (Cnidaria; Ceriantharia; *Isarachnanthus*) in the Atlantic Ocean. Plos One 7:e41091.

Stockwell D R B, Peters D P. (1999). The GARP modelling system: problems and solutions to automated spatial prediction. *International Journal of Geographic Information Science* 13 143–158.

Stockwell, D. R., & Peterson, A. T. (2002). Effects of sample size on accuracy of species distribution models. *Ecological modelling*, *148*(1), 1-13.

Suguio, K.; Martin, L.; Bittencourt, A. C. S. P.; Dominguez, J. M. L.; Flexor, J.-M.; Azevedo, A. E. G. (1985) Flutuações do nível relativo do mar durante o Quaternário superior ao longo do litoral brasileiro e suas implicações na sedimentação costeira. Revista Brasileira de Geociências, 15(4), 273-286.

Teece, M.A.; Estes, B.; Gelsleichter, E.; Lirman, D. (2011).Heterotrophic and autotrophic assimilation of fatty acids by two scleractinian corals, *Montastraea faveolata* and *Porites astreoides*. Limnology and Oceanography. 56, 1285-1296.

Tyberghein, L., Verbruggen, H., Pauly, K., Troupin, C., Mineur, F., & De Clerck, O. (2012). Bio-ORACLE: a global environmental dataset for marine species distribution modelling. *Global Ecology and Biogeography*, *21*(2), 272-281.

Weis, V.M., & Allemand, D. (2009). What determines coral health? *Science*,*324*(5931), 1153-1155.

Wisz, M. S., Pottier, J., Kissling, W. D., Pellissier, L., Lenoir, J., Damgaard, C. F. & Heikkinen, R. K. (2013). The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. *Biological Reviews*, *88*(1), 15-30.

Welk E, Schubert K, Hoffmann M H. (2002). Present and potential distribution of invasive garlic mustard (*Alliaria petiolata*) in North America. *Diversity and Distributions* 8, 219–233.

Yan, L. P., Li, S. F., & Ding, F. Y. (2004). The preliminary studies on the dynamics of macro-jellyfish resources and their relationship with fisheries in the East China Sea and Yellow Sea. *Marine Fisheries*, *26*(1), 9-12.

Yee, T. W., & Mitchell, N. D. (1991). Generalized additive models in plant ecology. *Journal of vegetation science*, *2*(5), 587-602.