Finding Ocean Giants: Using Species Distribution Modeling to Advance Our Understanding of *Architeuthis dux*

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I certify that I have read this thesis and that, in my opinion, it is satisfactory in scope and quality as a thesis for the degree of Bachelor of Science in Global Environmental Science.

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For all of the people who I never would have made it this far without, especially my family who provided me with the opportunity to pursue my dreams and my many mentors who inspired me to chase my passions, I could have never done it without them.

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ABSTRACT

The Giant Squid, *Architeuthis dux*, has been described for well over a century yet the majority of its life remains largely a mystery. They are known to have a global distribution with a prior study breaking them into three distinct populations, but the drivers behind their distribution remain unknown. In order to better understand their distribution and make inferences into their biology we created a species distribution model using Maxent. Records of occurrence were gathered from specimen databases from around the globe (-94 occurrences), and the model was developed using variables of sea surface temperature, net primary production, surface nitrate, surface phosphate, surface silicate, and averaged mesopelagic dissolved oxygen concentration. The model identified *A. dux* to have strong associations with areas of high productivity and exclusion from equatorial temperatures and oxygen minimum zones. In terms of ocean features, *A. dux* appears to associate most heavily with eastern boundary currents. These areas of likely occurrence are very productive regions and the presence of *A. dux,* a high trophic level predator in these regions has implications for developing understanding of these food webs and associated fisheries. Further improving our understanding of *A. dux* will require greater sampling for that purpose, which has become feasible due to new techniques in the field.

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1.0 INTRODUCTION

1.1 Development of *Architeuthis* Biology

Despite being originally described over a century and a half ago *Architeuthis dux* Steenstrup 1857, the giant squid, remains one of the most mysterious megafauna in the pelagic environment. The majority of their life history and ecology remains largely unknown. The few studies that have made preliminary attempts at describing the organisms ecology have been almost entirely based on a very small number of individuals due to the limited availability of specimens (Landman *et al,* 2004); (Coro *et al,* 2015). The rarity of specimens is due to multiple compounding factors. The first is the inaccessibility of *A. dux's* habitat, especially in earlier studies when specimens were almost exclusively collected via stomach contents of large toothed whales and floating/stranded dead squid. Even with modern technology, the large and very mobile giant squid has remained extremely elusive, with few live observations (Kubodera and Mori, 2005). Many of the specimens collected since the 1980's have occurred as bycatch in deep sea fisheries. With these few specimens, research has been conducted to try to ascertain characteristics of their life history and/or ecology. From gut content analysis the giant squid has been categorized as a high trophic level predator feeding on pelagic fish and cephalopods (Regueira, et al. 2013). The early life history of *A. dux* is practically unknown with an extremely limited sample of paralarvae (Jereb and Roper, 2010) and juveniles (Roper and Young, 1972) that derive from stomach content analysis of mesopelagic fish, but through stable isotope analysis of C^{14} from specimen's beaks there appears to be an ontogenetic shift in lifestyle, assumed to be the squid reaching maturity at about 2 years of age (Guerra, et al. 2010), with a potential maximum lifespan estimated at 14 years (Landman, et al, 2004). This is notable for being much longer than most squids which only live for 1-3 years (Hoving, et al. 2017), and is why this upper age range is potentially questionable. One indisputable characteristic of *A. dux* life history is their incredible fecundity with one female capable of carrying more than 6 million eggs (Hoving et al. 2004).

1.2 *Architeuthis'* Ecological Importance

Developing our understanding of the ecology of *A. dux* has potentially broad implications across its range. As mentioned earlier, individuals are now found most commonly as bycatch in deep sea fisheries. Fisheries notable for their presence of *A. dux* include hoki and orange roughy fisheries in the Southwest Pacific, (Jereb and Roper, 2010). The presence of a fast growing high trophic level, (Regueira, et al. 2014), predator in these fisheries has implications for their conservation and management due to potential top down effects that *A. dux* could exert in these fisheries. Conversely, *A. dux* could play a role in some ecosystems as a mid-trophic level prey item. This has been demonstrated by the identification of extremely rare juveniles in the stomachs of a mesopelagic fish, *Alepisaurus ferox* (Roper and Young, 1972), and the adults are believed to be regularly preyed upon by sperm whales (Jereb and Roper, 2010). The ecological role of large squids is well demonstrated in the Gulf of California where Humboldt squid play a major role in facilitating energy flow through the ecosystem, both as an adaptive predator and a large soft bodied prey item (Rosas *et al,* 2008).

1.3 Historical Understanding of Distributions

When it comes to *A. dux's* known distribution and the development thereof it is important to consider the history of our understanding of *Architeuthis'* taxonomy.

Originally, a variety of taxa were recognized across their global range as rare specimens resulted in many instances of the species being described under different names. These species were later synonymized into a convention recognizing three distinct species in the North Atlantic, North Pacific, and Southern Ocean respectively (Fig 1), although they have since been further synonymized into the single species *A. dux* with three subspecies for these distinct populations. There is still some debate about the level of differentiation between giant squid populations in the Atlantic, Pacific, and Southern oceans, however the most recent genetic analysis supports a single global species (Winklemann, 2013). Their vertical distribution has been another area of inquiry. From morphological analysis, especially of their unusually large eyes (Nilsson, et al. 2012), and accumulated records, *A. dux* appears to be broadly mesopelagic (Jereb and Roper, 2010). This has been corroborated by recent in situ sightings at mesopelagic depths (Kubodera and Mori, 2005), placing it at the depth junction between human use and the understudied deep ocean.

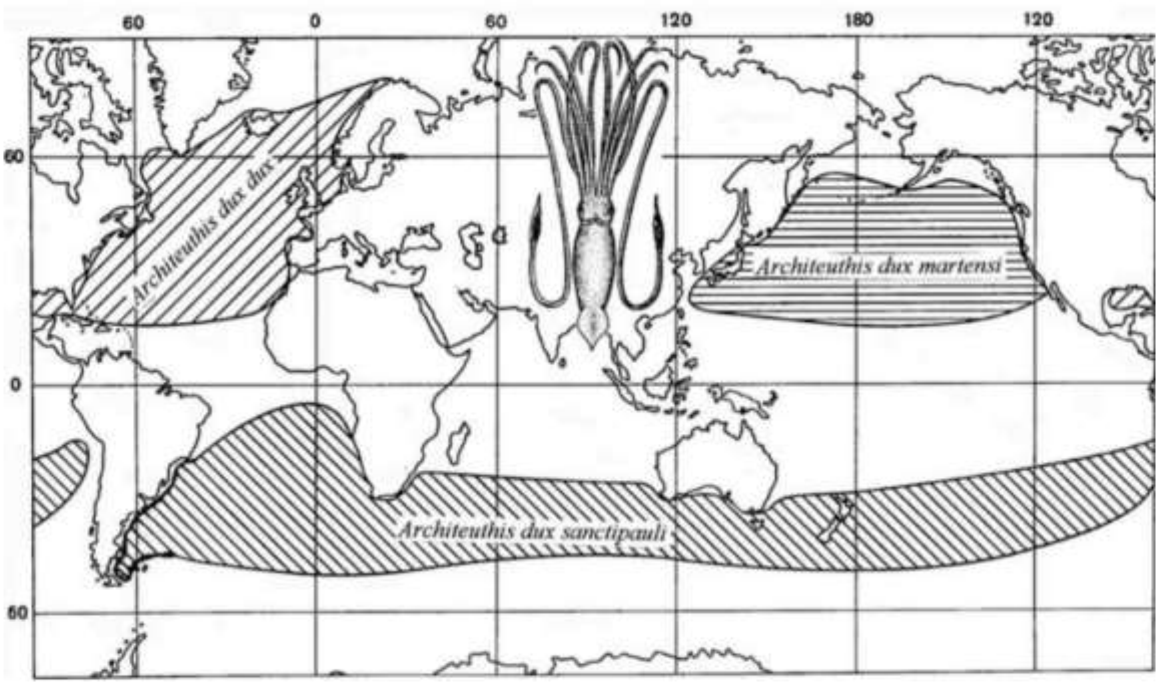

Figure 1: Illustrated figure of *Architeuthis* species' range from Nesis, 1985. Notable for future inquiry are the ranges of three subspecies, and the apparent absence of animals in equatorial and polar waters

1.4 Our Rationale

In order to expand our understanding of this elusive pelagic predator we developed a species distribution model to aid in defining the range and habitat of *A. dux*. Previous attempts to describe the habitat distribution of this species used a limited number of organisms, did not explore the importance of environmental variables, and were more concerned with the modeling methodology than the ecology of the organisms (Coro *et al*, 2015). By including a larger sample of squids globally a more robust distribution model can be developed that explores the importance of specific environmental variables. This is a first step in understanding the biology pf *A. dux,* and maybe better direct inquiry in studying other aspects of its biology and ecology. The model could be used to evaluate if the three populations have discrete habitats.

2.0 METHODS

2.1 *Architeuthis* Occurrences

Global occurrences of giant squid were gathered from the Ocean Biogeographic Information System (OBIS, 2018) and the Global Biodiversity Information Facility (GBIF, 2018). Not all samples in these data sets were useable, with a minimum requirement of location data with precision of at most +/- 1 kilometer. Records were cross-checked for repeat occurrences both between and within databases. This was done by comparing time and location data wherever possible. Further potential errors were investigated by plotting occurrences by their location data to visually inspect all occurrences, with some occurrences being removed due to repeat records by coordinates that occurred not in an ocean.

2.2 Modeling Program Selection

A habitat distribution model for the giant squid was generated using the program Maxent, a maximum entropy species distribution and niche modeling program (Philips et al. 2018). Maxent was selected due to its focus on modeling based on presence only data as well as its previous success modeling the distributions of rare species (Coro *et al*, 2015). Maxent uses presence data along with selected environmental variables in a machine learning process to generate and test a distribution (Elith, et al, 2011).

2.3 Selection of Environmental Variables

The environmental variables selected to develop the habitat profile for *A. dux* needed to have a global distribution and relevance to the biology of the species. This limited the available predictors and I settled on average sea surface temperature (SST) (Locarnini, et al, 2018), surface nitrate, surface phosphate, surface silicate (Garcia, et al, Nutrients, 2018), net primary production, and averaged mesopelagic dissolved oxygen (Garcia, et al, Oxygen, 2018). Environmental variables were collected primarily from World Ocean Atlas 2018 at a resolution of 1 degree across a global distribution for all variables. The selection of SST was a result of analyzing previous distribution maps for the species which clearly note their absence from tropical and polar waters (Nesis, 1985) and use of mesopelagic temperatures reduced model fitness in all runs. These latitudinal trends suggest temperature may play an important role in *A. dux's* habitat. The suite of surface nutrient concentrations along with NPP were selected as relevant variable due to the giant squid's known role as a higher trophic predator as stated previously. It can then be inferred that in order to support such large and high trophic level predators, overlying productivity likely must be high, making these variables potentially critically important. Finally mesopelagic oxygen was selected due to potential competing theories. Conventional thinking would lead to a conclusion that the large aerobic predator would be limited by low dissolved oxygen as oxygen minimum zones are known to exclude some taxa (Sutton, 2017). However there are comparable species of squid, such as *Dosidicus gigas*, that have adapted to exploit oxygen minimum zones (Fields, et al. 2013). Thus *A. dux's* modeled relationship with dissolved oxygen may give insight into its physiology and ecology. These variables were used in a climatological fashion; variables were used at longest available temporal averages to attempt to account for the wide range of occurrence data through time. Environmental data were sampled in two dimensional layers using, the program Ocean Data View (Schlitzer and Reiner, 2018).

The exception to this process was oxygen data. Surface oxygen would likely be irrelevant to *A. dux* and is frequently saturated. Therefore, oxygen data in *A. dux's* mesopelagic habitat, from a depth range of 200m to 1000m were averaged to capture the extent of the oxygen minimum zones and then interpolated to fill areas of missing data for both the water column and geographic regions. For Maxent, all data layers must have the exact same geographic resolution, an issue that arose with gaps in such large data sets or extra data superfluous to this project's purpose, such as temperature data from the Black Sea and Caspian Sea. To resolve this issue, all layers were combined in one dataframe and then subset so only points with data in all variables were kept. When visually inspected, this resulted in all layers having consistent coverage across the major ocean basins.

2.4 Maxent Model Conditions

With occurrence data and environmental variables formatted, a Maxent model was run using 70% of *A. dux* occurrences to test the model and using 500 iterations. 30% of the occurences were reserved to test the model. This test is used to evaluate model accuracy by generating a specificity versus sensitivity curve, in which the area under the curve (AUC) compared to a random distribution can be evaluated as a form of model fit. Along with the species distribution projection, the Maxent model also creates response curves. These alter each variable while holding the other environmental variables constant. This approach allowed us to analyze the importance of each variable across its range as it interacts with other variables. Finally, we execute jacknife tests to determine the significance of each variable, assessing their explanatory power by determining which variables hold the most information overall and which hold the most unique information not present in the other variables.

3.0 RESULTS

3.1 Specimen Characteristics

An original goal of this project was to attempt to integrate as many giant squid unique occurrences as possible. The number of verifiable unique occurrences was 186 individuals. If the basis of record included details of the individual, these characteristics were briefly analyzed across this large cross section for this species. However beyond location data there was quite commonly missing information due to many confounding factors such as differing basis of the record, differing procedures, etc. From Figure 2, it is clear that the majority of specimens are adults falling between one to two meter dorsal mantle length (DML), with few above that threshold. There are also smaller individuals present that may be *A. dux* juveniles or paralarvae. Notable areas of relatively high occurrence are visible in Figure 3. (Japan, Southeast Australia, New Zealand, South Africa, and the Gulf of Mexico) as are areas of relatively low occurrence or total absence (equatorial regions globally and broadly the Pacific, northern Indian ocean). Figure 4 demonstrates *A. dux's* broad mesopelagic range, however this information somewhat complicated by the inclusion of records of individuals near the surface who may not be healthy and that many depth recordings come from individuals collected by trawling, with the specific depth of capture often impossible to determine. We also plotted the occurrences through time, and while not all specimens had an associated date, the majority of the occurrences have been since 1990 (Fig 5).

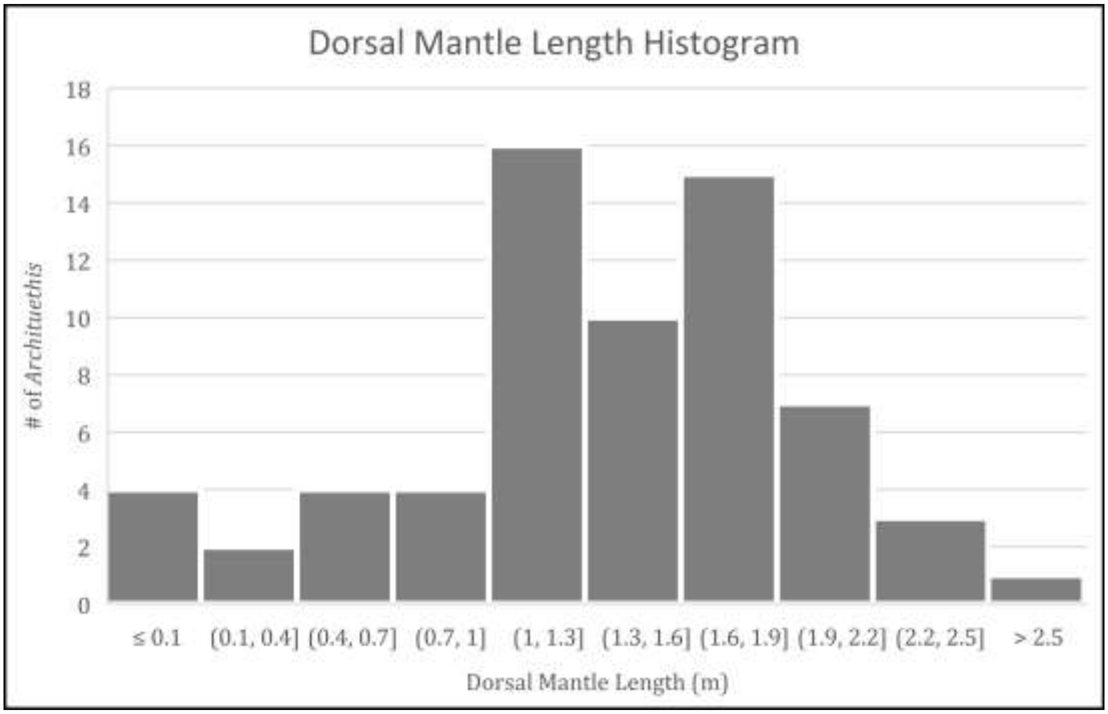

Figure 2: Histogram of Dorsal Mantle Length (DML) for *A. dux* specimens binned at 30 cm intervals (n=66). Subset of all occurrences where this data was collected.

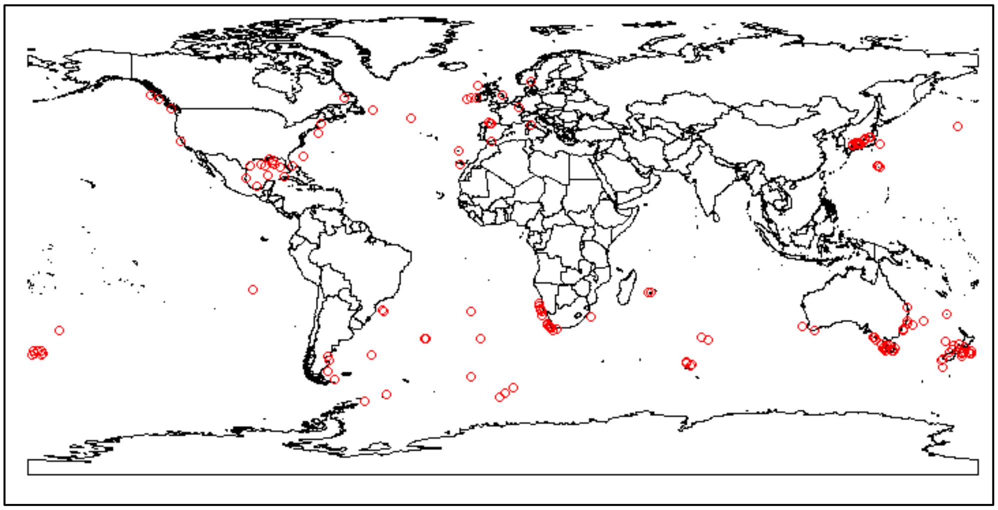

Figure 3: Map plotting all positionally reliable occurrences (n=186).

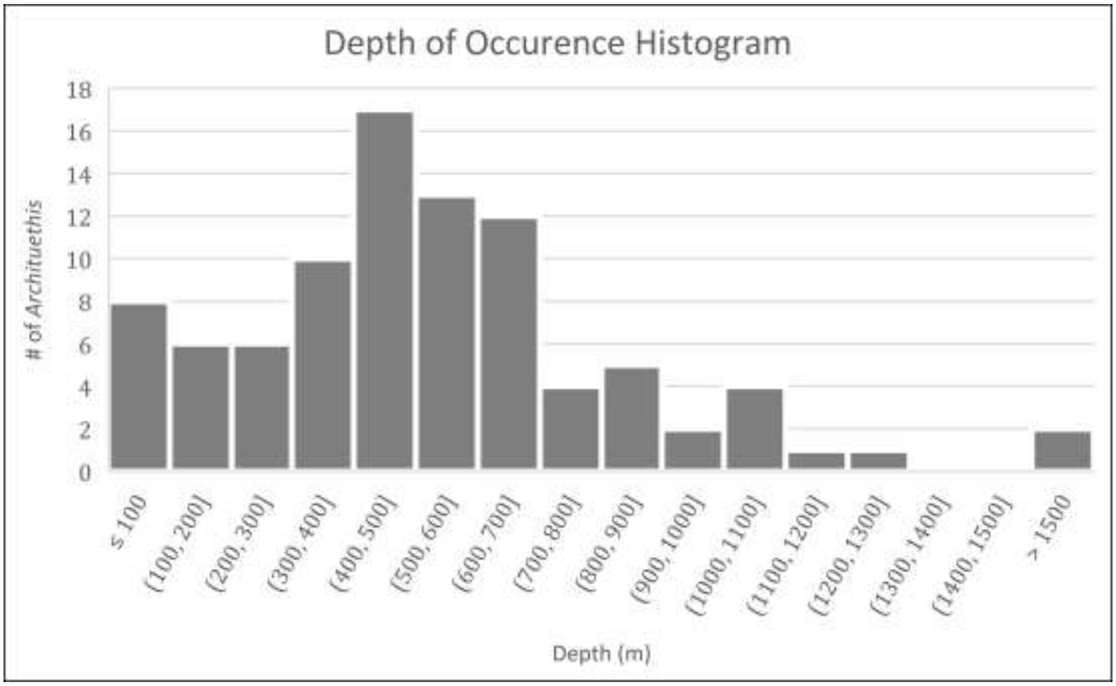

Figure 4: Histogram of recorded depth of occurrence by 100 meter increments (n=91).

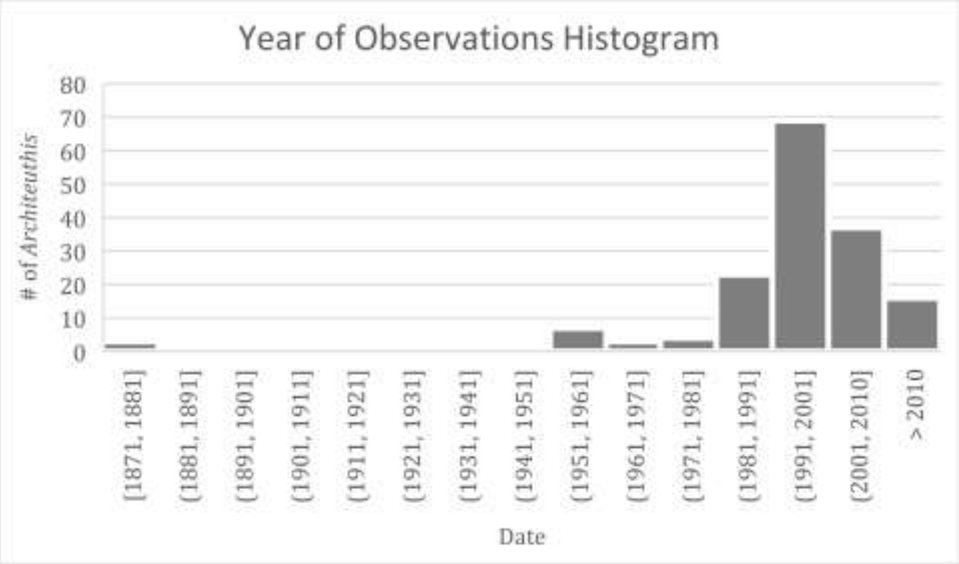

Figure 5: Histogram of occurrences through time (n=166).

3.2 Environmental Variables

Sea surface temperature (Fig. 6) has the clearest trends of the environmental variables, with the highest temperatures at the equator with temperature falling as you move poleward. Also visible are some surface currents, especially boundary currents as they deliver warm water poleward or cool water towards the equator. Plotting NPP (Fig. 7) allows the inspection of areas of relatively enriched production mainly upwelling regions, both coastal and equatorial, along with enriched production in higher temperate latitudes while the center of ocean gyres are relatively unproductive. All three nutrient concentrations have somewhat similar trends (Fig. 8) with enriched concentrations in the Southern Ocean and lower concentrations elsewhere across the globe. Finally, inspecting a plot of mesopelagic oxygen concentrations identifies major OMZ regions with the most significant and extensive one in the Eastern Tropical Pacific and the least in the Eastern Tropical Atlantic. Also as a result of subsetting to ensure consistent spatial coverage for all data types, there was a loss of data in some area, primarily in shallower regions, reducing resolution in more enclosed marine areas. This procedure also significantly reduced the number of specimens used in the model, although the total number remains very high relative to the number used in most studies focused on *A. dux* and coverage was not reduced in areas with already low numbers of occurrences (Figure 9).

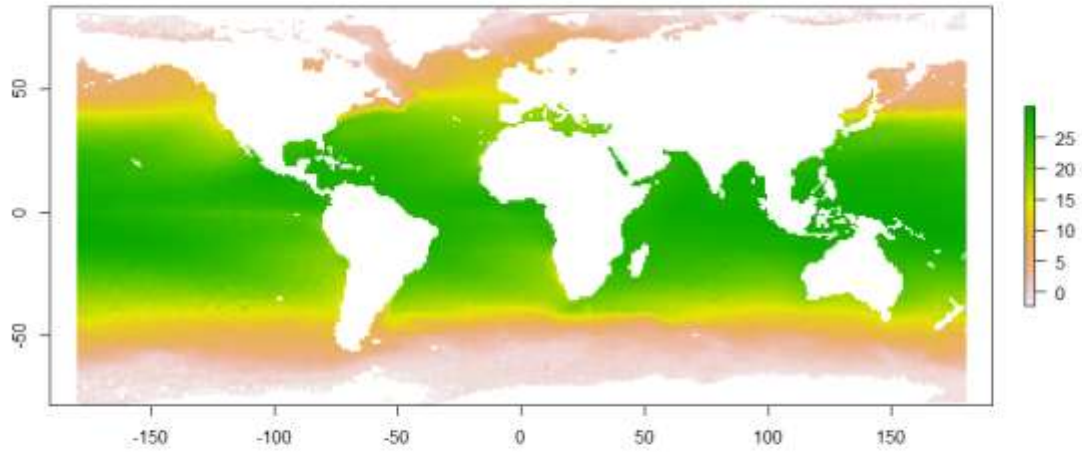

Figure 6: Plot of Sea Surface Temperature Variable Layer in degrees C

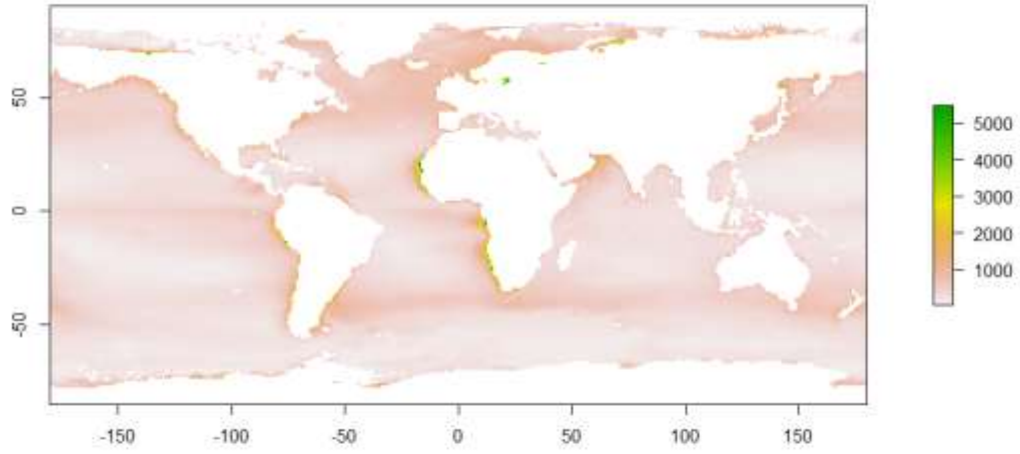

Figure 7: Plot of Net Primary Production Variable Layer in (g C/m^2*yr)

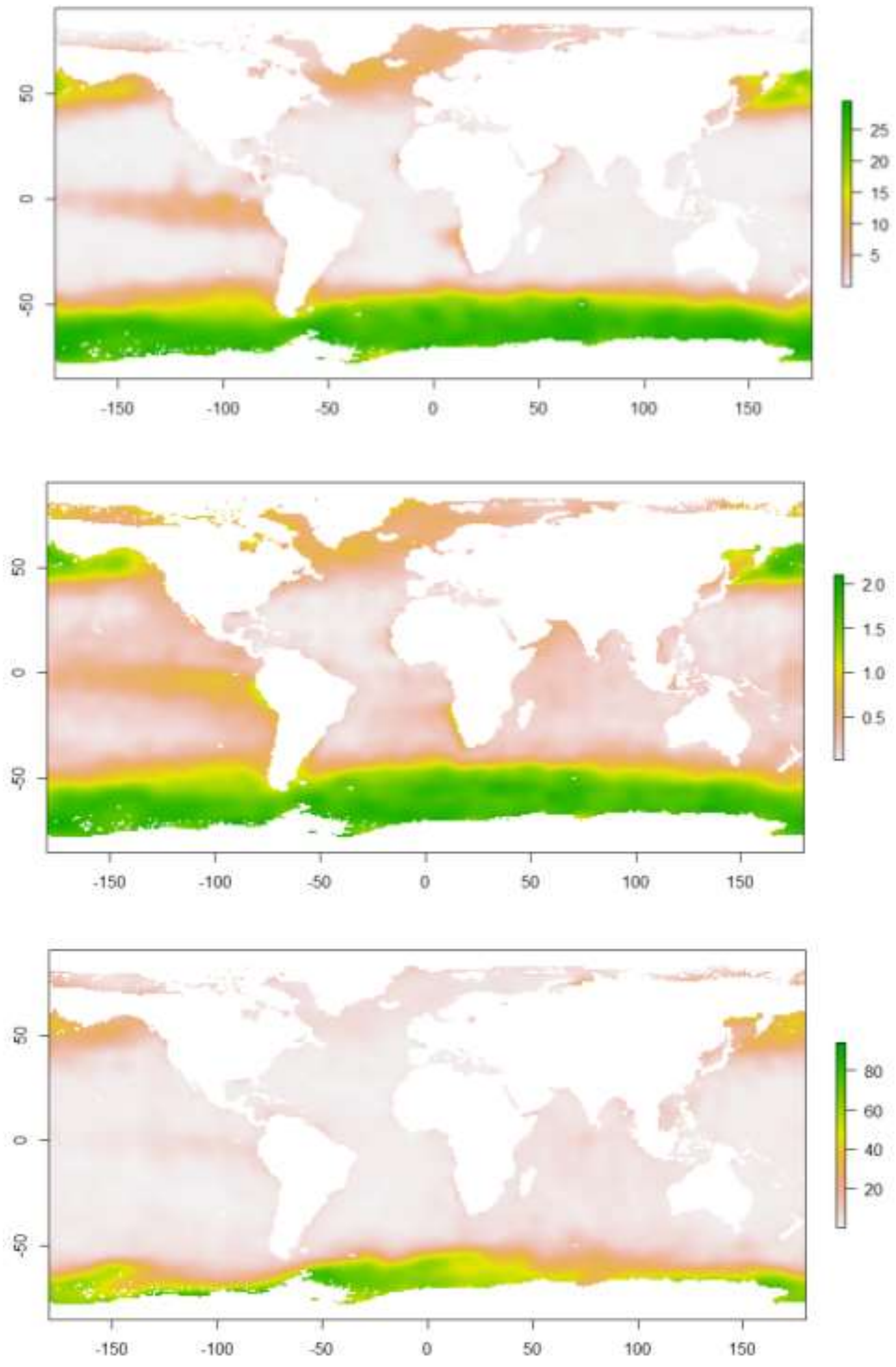

Figure 8: Plots of Nitrate, Phosphate, and Silicate reported in mmol/kg

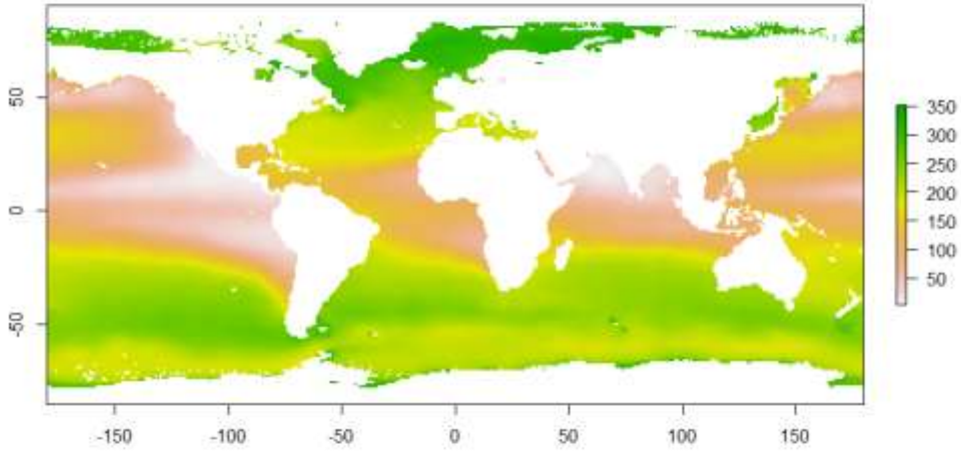

Figure 9: Plot of integrated mesopelagic oxygen (mmol/kg).

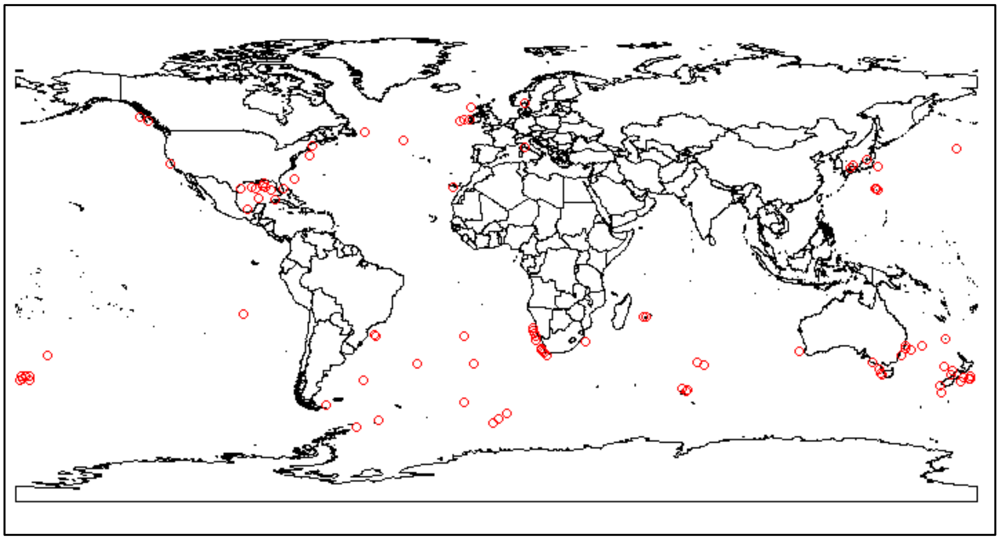

Figure 10: Map of *A. dux* specimens used in the final model (n=94).

3.3 Species Distribution Model

With this set of 94 occurrences and environmental variables, the Maxent model generated a distribution map indicating the probability of occurrence of giant squid over the global ocean (Fig. 11). Confidence in the species distribution model generated for *A.*

dux was relatively high with a test AUC of 0.853, well over the totally random 0.5 (Fig 12). This suggests the model has high predictive power for these samples. Large swaths of open ocean where occurrences are modeled to be likely have relatively few occurrences, most notably the North Pacific and Southeast Pacific.

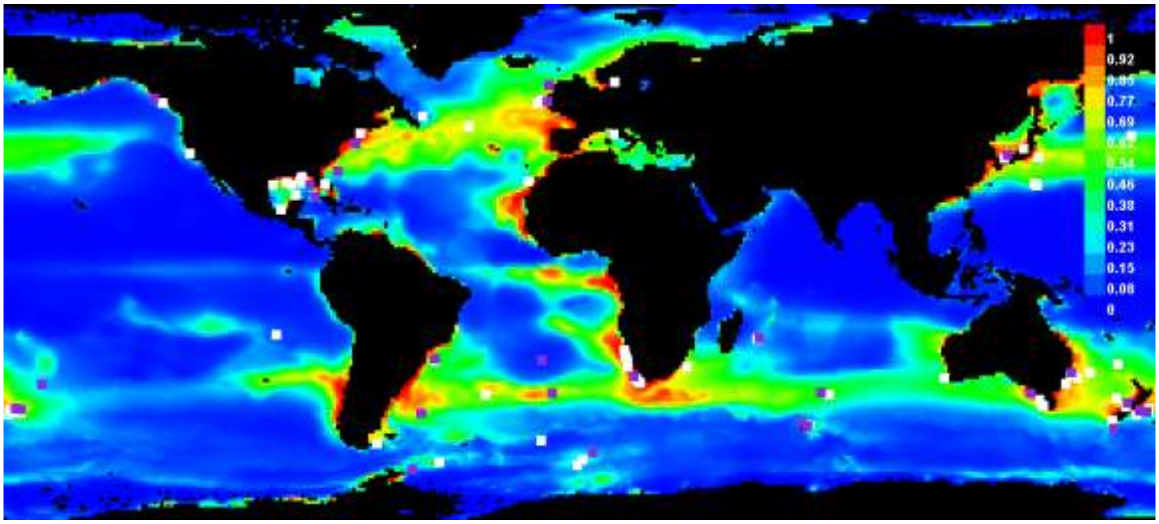

Figure 11: Model of *A. dux* species distribution, with hot colors predicting a high likelihood of occurrence and cooler colors predicting lower likelihood of occurrence (n=94). The white squares are occurrences used in model training and the purple squares are a randomly selected 30% for testing.

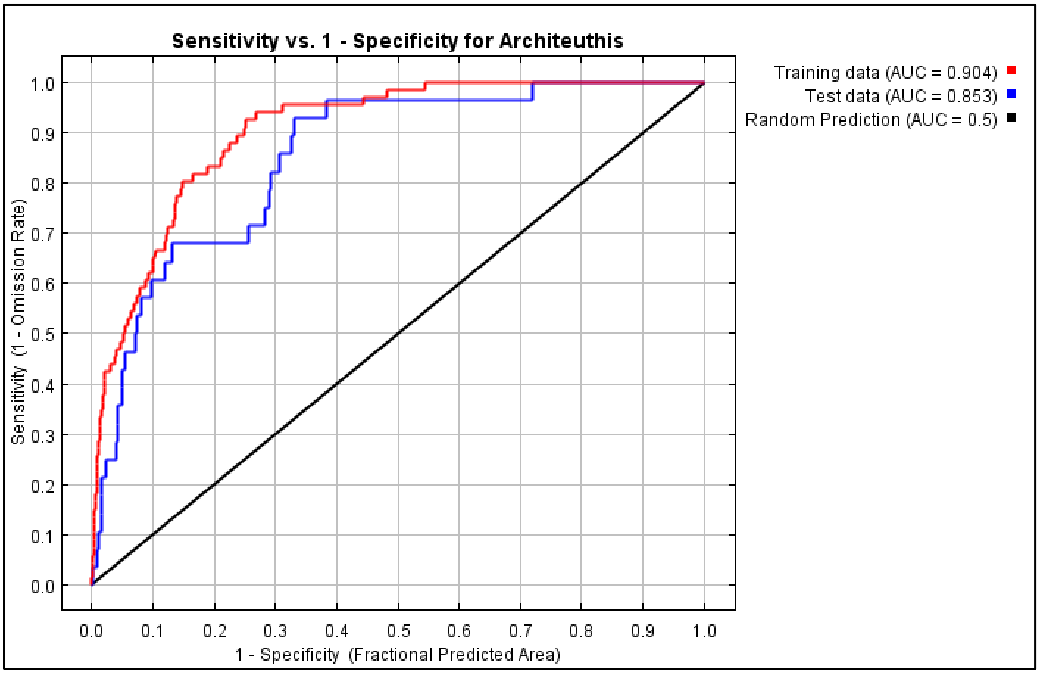

Figure 12: A plot of the receiver operating curve for training and test data. The AUC is a metric of how well the model predicts the distribution of the species relative to a random distribution, the black line.

3.4 Measuring Variable Importance

First and foremost amongst the variables is Net Primary Production (NPP), which in nearly every analysis proved to have the most descriptive power out of all the variables. The relationship (shown in Fig. 15) is quite clear, this large and fast growing predator is likely to occur in areas with the energetic resources to support it. A less clear signal can be seen in the role of mesopelagic oxygen. In Fig. 13, it appears that mesopelagic oxygen concentration is a poor predictor on its own for *A. dux's* distributions, however the run where it was excluded shows a larger drop in AUC than the nutrient variables, Nitrate and Phosphate, which performed better as predictors in isolation. This relationship is clarified in Table 1, where mesopelagic oxygen was the second greatest contributor, suggesting it contains information that is significant when used in conjunction with other variables. The three nutrients included, Nitrate, Phosphate, and Silicate had very minimal impact on the model. This can be seen in Table 1 where their percent contribution and permutation importance is extremely low, as well as in the tests without these variables in Fig. 13 where their exclusion appears to be almost inconsequential.

Table 1: Determining Variable Importance by their contribution in the training gain and then by randomizing their values and measuring their drop in AUC as a result of the permutation.

Variable	Percent Contribution	Permutation Importance
Net Primary Productivity	57.4	46.4
Mesopelagic Oxygen	20.3	16
Surface Temperature	15.8	24.4
Surface Nitrate	3.2	4.2
Surface Phosphate	0.3	5.4
Surface Silicate	2.9	3.6

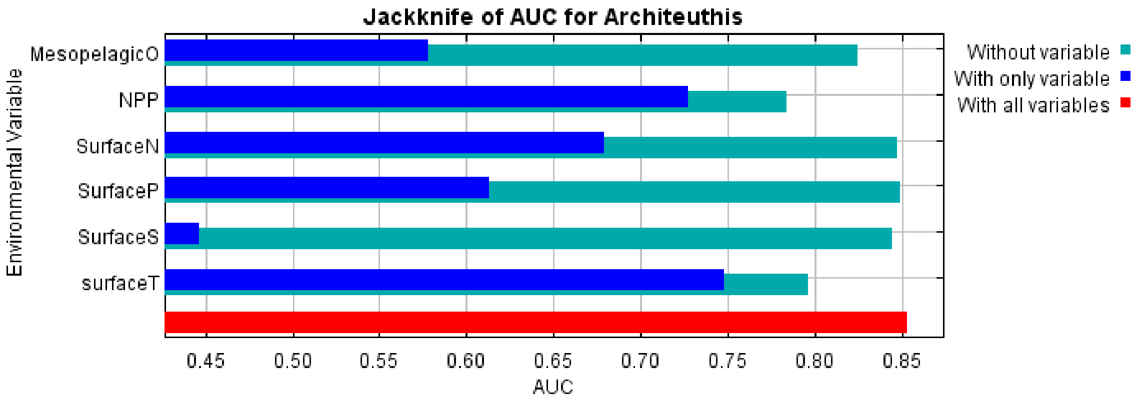

Figure 13: A jacknife test to determine variable importance whereby variables are used in isolation and excluded in order to determine which variables have the most information and those with the most unique information.

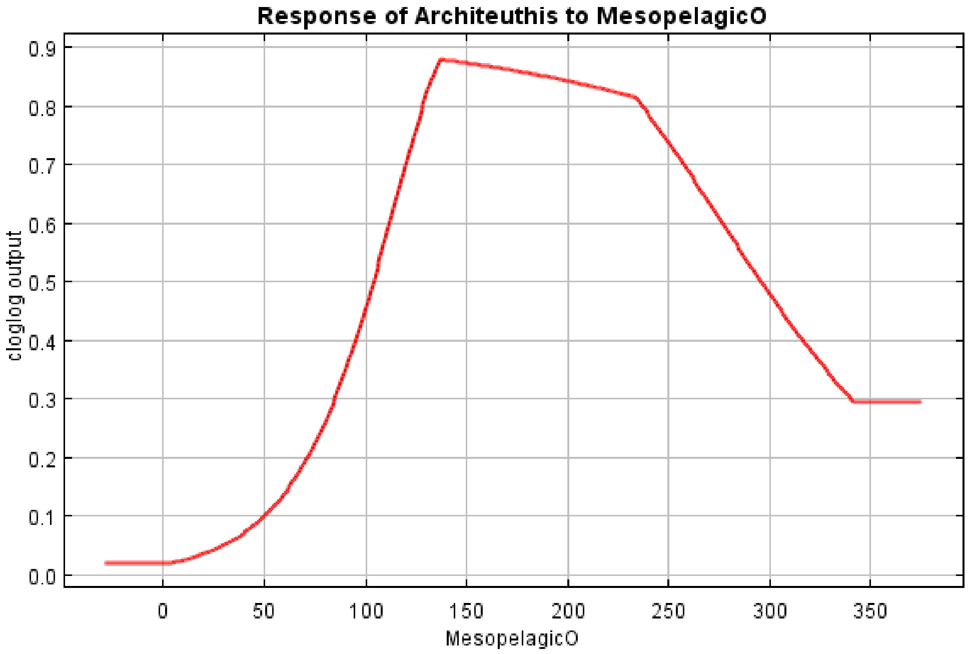

Figure 14: Response curve for *A. dux* with averaged mesopelagic dissolved oxygen (mmol/kg).

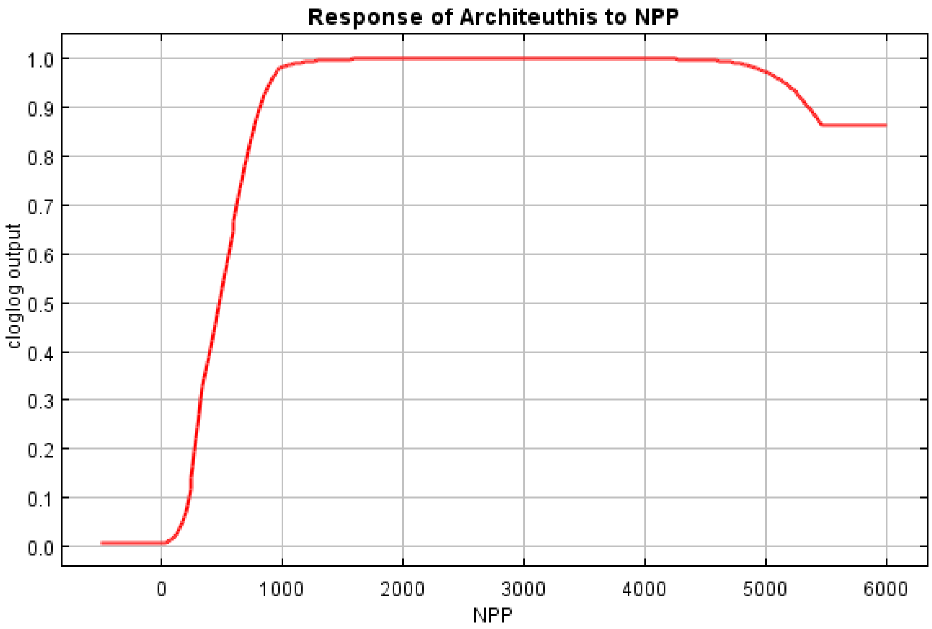

Figure 15: Response curve for *A. dux* with net primary production (g C/m^2*yr)

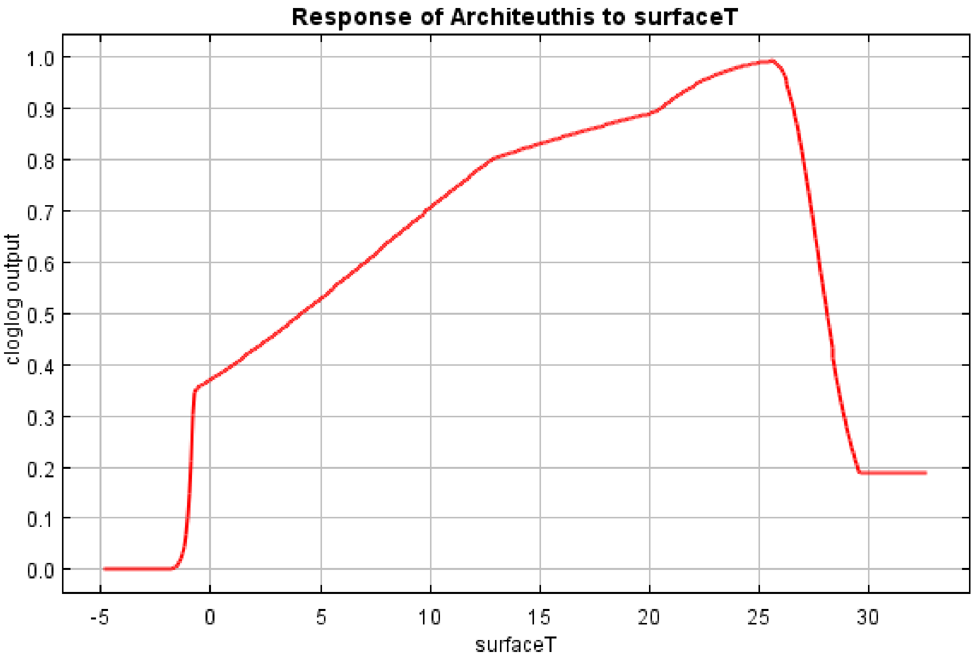

Figure 16: Response curve for *A. dux* with Sea Surface Temperature (C)

4.0 DISCUSSION

4.1 Model Accuracy

The model appears to have high descriptive power for these occurrences, however an implicit part of the model should be considered. The potential remains that this set of occurrences is a biased data set, with the majority of giant squid being found in relatively close proximity to shorelines. Resolving the potential role of sampling bias would require more random sampling for *A. dux* across the ocean basins, a task which up until recently would have required massive tows or other dedicated efforts, making such a project unfeasible and prohibitively expensive.

4.2 Interpretation of Variables

The one case where NPP was not the best predictor was when it was run in isolation for the jacknife (Fig 13), which when compared to the other variables SST performed marginally better. This variable had the third highest percent contribution but the second highest permutation importance in Table 1, a reflection of its importance as when values are randomized and the latitudinal trends it reflects are lost, the descriptive power of the model suffers considerably. The variable's relationship in Fig. 12 shows Architeuthis' tendency towards warmer waters, until the significant reduced likelihood of occurrence in equatorial regions, which can be verified with Figure 6.

. Fig. 13 is most interesting for confirming the original rationale for including mesopelagic dissolved oxygen in the model, with very low values of this variable appearing to limit *A. dux's* distribution. This can be seen in the modeled species distribution as it predicts giant squid's absence from the strong OMZ in the Pacific. We know large active squids have high oxygen demand, excluding them from occupying regions of low oxygen (Pörtner, 2002) and this result allows us to confirm that *A. dux* is not an exception to this trend.

The three surface nutrient variables appear relatively unimportant for the model, providing little in the way of new information. An explanation for these variables poor descriptive power is that the factor they were attempting to capture is far more usefully present in NPP.

4.3 Qualitative Model Assessment

One of the most interesting broad trends in the model that is immediately apparent is the emergence of bands of predicted occurrence in the N. Atlantic, N. Pacific, and broadly Southern Ocean, as illustrated in the three-species hypothesis (Nesis, 1985). Our results therefore potentially lends some credence to the idea that there could be discrete stocks of *A. dux*, although a recent genetic study (Winklemann, 2013) found little evidence for genetic differentiation among these regions and inferred that significant gene flow may occurs through the global ocean.

A geographic feature in the model that requires some explanation or investigation is the band of high predicted occurrence in the equatorial Atlantic, despite there being no known occurrences within 15 degrees of the equator. A potential explanation of this is a conjunction of mesopelagic oxygen and NPP variables. With the high descriptive power of NPP, it becomes potentially overpowering in the region of equatorial upwelling, despite the high SST. Mesopelagic oxygen plays a role in mitigating this effect in the Pacific, where NPP is still high but it does not experience the same high predicted occurrence potentially due to the more pronounced oxygen minimum zone (Paulmier and Ruiz-Pino, 2009). In contrast, the younger deep water in the Atlantic is less oxygen deficient, reducing the mitigation effect of these variables working in conjunction and resulting in an overestimation. The relationship with dissolved oxygen explains features of the model, with dissolved oxygen across the Eastern Pacific being potentially limiting to *A. dux*, limiting their access to those productive regions. As previously discussed, dissolved oxygen is known to be a limiting factor for large active squids (Pörtner, 2002), however not for all squids, such as *Dosidicus gigas* who has been noted for its association with these midwater features (Gilly, et al. 2006). Despite potential for *A. dux*'s predicted occurrence being the result of a model artifact, it is possible instead that the less pronounced OMZ in the Atlantic does not limit their distribution and the lack of equatorial samples is more related to much lower sampling effort in the region.

When focusing on areas of highest likelihood of occurrence we see association most heavily with a specific oceanographic feature, western boundary currents. These currents bring warm waters towards the poles while stimulating high productivity (Everett and Doblin, 2015), both conditions favorable to *A. dux*. Further, oxygen minimum zones are most associated with the eastern side of basins (Fig 9), so low midwater oxygen is not generally a concern within these currents. These factors make western boundary currents appear to be optimal conditions for *A. dux*, which is especially notable for the ecology of these regions due to their productivity and as a result the fisheries in these regions (Everett and Doblin, 2015). The unrecognized presence of a high trophic level predator has interesting implication for these fisheries.

4.4 Potential Role of Timescale

As previously discussed, the environmental variables were used at annual mean values averaged over long time scales in order to integrate with the somewhat dispersed collection of occurrences. While this was necessary for the model, the approach minimizes a significant amount of informative nuance that could help fill in gaps about *A. dux*’s ecology and habitat profile. Part of why we believe *A. dux* may respond strongly to shorter timescale events comes from their reproductive and developmental biology. As mentioned previously they are incredibly fecund (Hoving, et al. 2004) and fast growing (Guerra, et al. 2010), a similarity they share with other species of large squid that have been well documented engaging in sudden range shifts to exploit favorable conditions (Field, et al. 2013). The first most immediately apparent temporal variable that almost certainly plays a role is seasonality, with a research group very recently providing support for the idea that *A. dux* is only in Japanese waters in the winter (Wada, et al. 2020). Considering the species documentation in the N. Atlantic, it would be interesting to attempt to investigate possible links with their distribution in the Atlantic with respect to the formation of cold core rings and the potential for opportunistic foraging from the enhanced production (Wiebe, 1982)

4.5 Continuing the Search

The most significant step we can take to advance our understanding and improve future attempts to elucidate the habitat of *A. dux* is to search more thoroughly across poorly sampled areas, outside the reach of deep-sea fisheries. Such a recommendation is not very realistic given the size of the nets required, the associated costs of trawls and/or cameras to find specimens, but a new method has emerged. Thanks to advances in environmental DNA (eDNA) techniques, positive detection of *A. dux* has been accomplished from water samples taken at a depth of 100 meters off Japan (Wada, et al. 2020). This technology could significantly reduce the potential cost for the search for the giant squid, allowing the potential advancement of projects to investigate the temporal, geographic, and vertical distribution of the species at resolutions that would otherwise be impossible. eDNA methods, could also provide information on both presence and absence, expanding the range of modeling options beyond those reliant on presence only. These models could include Generalized Additive Models, and Boosted Regression Trees, models dependent upon presence absence that could be used to further test the robustness of the trends and patterns of the distribution of *A. dux* (Moore, et al. 2016). Using these techniques we could search for *A. dux* especially in regions of overlap between fisheries and regions of prior or suspected occurrences such as in the Brazil Current and in regions of suspected occurrence but low traffic such as the eastern extent of the Kuroshio Current. These data could be used to determine if the giant squid plays a role in these ecosystems and if so understanding the ecology of *A. dux* may become a greater priority for fisheries management across the species range.

5.0 CONCLUSION

The giant squid, *A. dux*, may be a globally distributed species but the original three population model does appear to hold some merit. Using modern machine learning principles through a Maxent species distribution model allowed the most comprehensive view of this species' distribution, notably its association with productive ecosystems and its potential exclusion from low oxygen zones. For work to continue in advancing our understanding of the species more robust and random sampling must occur across areas that are currently major occurence gaps to test the current distributions. Such tests are now possible thanks to recent advances in the field.

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