A modelled global distribution of the kelp biome

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A modelled global distribution of the kelp biome

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Abstract
Kelp, seaweeds of the order Laminariales, are of ecological and conservation importance because they form undersea forest habitat for many varieties of fauna and flora including mammals, and commercial fish species. In the absence of a world map of the kelp biome, we predicted its potential distribution using geographic records and environment variables in a MaxEnt model. This estimated that the kelp biome occupied 1,469,900 km^2 and was present on 22 % of the world's coastline. While average sea surface temperature was the most important environmental variable for the biome across all species, wave height, distance from the coast and minimum temperature were of most importance for individual species. This map can be used in planning where marine reserves should be best located, modelling the effects of climate change, and in estimating the blue (ocean) carbon storage. Current field observations should confirm the presence of kelp within the modelled biome, and if absent consider if human impacts, including climate change, are to blame.

Introduction
The kelp biome is comprised of over one hundred species of habitat-forming seaweeds of the order Laminariales many of which form forests on shallow rocky seabed's in temperate and subpolar seas, and a few deep cold tropical locations (Steneck et al. 2002; Graham et al. 2007; Krumhansl et al. 2016; Wernberg and Filbee-Dexter 2019; Jayathilake and Costello 2019). The complexity of the three-dimensional structure of the kelp biome provides habitat for a diversity of species, including commercial fish (Teagle et al. 2017; Vásquez et al. 2014) and mammals of conservation importance (e.g., Markel and Shurin 2015). Kelp forests are the dominant primary producers in cold-temperate rocky reef ecosystems (Krumhansl and Scheibling 2012; Krumhansl et al. 2016) and amongst the most productive vegetation in the world (Mann 1973). Not only does kelp have indirect benefits to society by virtue of its ecological importance, but some species provide food for people (Stévant et al. 2018; Peteiro and Freire 2012). Kelp forests, and thus their associated fauna and flora, are threatened by harvesting, diseases, herbivory, competition from non-native species, storms, climate change, pollution, and the combined effects of these factors (Steneck et al. 2002; Wernberg et al. 2011; Krumhansl et al. 2016; Wernberg et al. 2019). Maps are thus useful to indicate the potential area that could be occupied by kelp species from local to global scales and facilitate conservation of kelp and its associate faunal and floral communities.

Even though kelp does not have a root system to store carbon in sediments like in the seagrass and mangrove biomes, or a calcareous skeleton as in the zooxanthellate coral biome, the "blue" (ocean) carbon in kelp can be transformed to other food webs through herbivory and detrital pathways (Krumhansl and Scheibling 2012; Alongi 2018). Algal carbon sequestration occurs primarily through the burial of dead algae in sediments, and 82% of kelp productivity is estimated to become detritus (Krause-Jensen and Duarte 2016, Krumhansl and Scheibling 2012). However, the amount of carbon that is being stored by kelp alone and contributing to the carbon cycle of the ocean has not yet been quantified (Krause-Jensen and Duarte 2016; Duarte 2017). The global area of kelp occurrence is an important factor in this calculation.

To date, there is no existing map that can be used to calculate the global distribution of the kelp biome. A few hand-drawn maps have shown the distribution of the kelp genera *Macrocystis, Nereocystis, Laminaria, Lessonia* and *Ecklonia* (Raffaelli & Hawkins 1999); and *Laminaria, Saccharina, Macrocystis, Nereocystis, Lessonia, Ecklonia* and *Eularia* (Wernberg et al. 2019). While useful to get an idea of the distribution of kelp, these maps cannot be used to calculate the biome area. Local-scale species distribution models have mapped the present distribution of kelp species and long term changes of kelp cover (Raybaud et al. 2013; Espriella et al. 2019), and locations of deep water tropical kelp refugia (Graham et al 2007). However, none of these studies have developed a polygon layer of the global distribution of kelp biome that can be used in geographical information systems (GIS). The availability of the kelp biome map has proved useful in the identification of the most suitable places for marine protected areas (Zhao et al. 2020), and could contribute to detection of change in kelp distribution due to ocean warming.

This study fills this research gap by modelling the global distribution of kelp biome using field records and environmental variables to provide a world map of this ecologically important biome. The combination of observed locations of species and knowledge of their environmental preferences enables the use of species distribution models to more comprehensively map this biome. The availability of such a global map will illustrate the importance of the kelp biome in global biodiversity, and enable improved estimates of global primary production, blue carbon budget, and deforestation rates. Further, this map will be useful for mapping the distribution ranges of kelp associated fauna.

Methods

Species occurrence data

The common term kelp typically refers to the order Laminariales. However, sometimes some large brown algae in the order Fucales, such as species of the genus *Durvillaea,* are included (Dayton 1985; Fraser et al.2009; Wernberg and Filbee-Dexter 2019). The present study was limited to the order Laminariales, which has 59 genera and 147 species (Guiry and Guiry 2018). Kelp distribution data were extracted from the Global Biodiversity Information Facility (GBIF 2017) and the Ocean Biogeographic Information System (OBIS 2017). Initially, we downloaded 109,824 occurrence records for the order Laminariales in 145 datasets from GBIF, and 47,695 records in 99 datasets from OBIS (SM Appendix 3). Prior to analysis, taxonomic names were reconciled with AlgaeBase (Guiry and Guiry 2018; Guiry and Guiry 2020; Horton et al. 2020). Since our analysis, *Chorda filum* has been removed from the Laminariales into the new brown algae order, Chordales but is still included in our dataset (Starko et al. 2019; Guiry and Guiry 2020). Data were available for 70 species belonging to 5 families (Table 1). We limited the model training dataset to data collected from 1900 to 2017 because species identification and geo-referencing were likely to be more accurate since then. Of the data used, 86% were sampled between 1970 and 2017. Records of fossil specimens, ambiguous locations according to comments in the dataset (e.g., drift material), and records with coordinate uncertainty > 10 km and falling on land, were removed. Multiple records for a species at the same location (i.e., identical latitude and longitude), including duplicates from both databases, were reduced to one record for that location (Fig. 1). We excluded 112,890 (72%) data points from the analysis as being questionable. The dataset used in this study can be downloaded from Figshare (Jayathilake and Costello 2020a). In addition, we have downloaded and mapped more recently published data from the GBIF (temporal scale from 2018 to 2020; spatial scale 90 N to 90 S and 180 E to 180 W) to assess the accuracy of the predicted model. This was prepared following the same procedure to use as the accuracy assessment dataset and is also available on Figshare (Jayathilake and Costello 2020b).

Environmental data

We obtained the environmental data from Global Marine Environment Datasets (GMED) (Basher et al. 2014b; Basher and Costello 2019). These data layers represent annual averages calculated over decades and thus indicate long-term characteristics of the environment (Basher and Costello 2019) (Table S1). GMED environmental layers have a 5 arc-minute resolution which is approximately 9.2 km at the equator (Table S1). For this study, a finer spatial resolution was needed to get more accurate distributions. Therefore, we re-interpolated the GMED data to 30 arc-second resolution which is approximately 1 km at the equator. All the interpolated raster layers were cropped to a 0 to 1000 m depth layer to reduce the computational time. The deepest at which any species of kelp has been found to be living is 90 m for *Laminaria rodriguezii* in the Adriatic Sea (Žuljević et al. 2016). Deeper records may be due to the sinking of kelp from shallow depths following detachment due to storms. Graham et al. (2007) predicted that the maximum depth for any kelp species would be 236 m in tropical deep waters. Thus, the present study extended well beyond the deepest likely range of kelp.

Previous studies focused on the influence of single abiotic variables such as temperature, wave exposure, water motion, salinity, light availability, dissolved oxygen, pH, nitrate and phosphate on the natural distribution of one or a few kelp species (Dayton 1985; Graham et al. 1997; Gerard 1997; Hurd 2000; Gaylord et al. 2002; Steneck et al. 2002; Wernberg and Thomsen 2005; Smale et al. 2013; Žuljević et al. 2016; Wernberg et al. 2019). Here we selected almost all the abiotic variables from previous studies to study which variables most correlated with the distribution of kelp, noting that many variables are also correlated with each other (Table S2). A preliminary MaxEnt model was run with 19 environmental variables (mean sea bottom temperature, calcite concentration, depth, diffuse attenuation coefficient, dissolved oxygen concentration, distance from the land, nitrate concentration, pH, phosphate concentration, photosynthetically active radiation, average sea surface temperature, maximum sea surface temperature, minimum sea surface temperature, range of sea surface temperature, salinity, silicate concentration, slope, surface current, and wave height) for each species, genus, family and all kelp (Tables 2). However, the variables calcite, minimum and range of sea surface temperature, mean sea bottom temperature, surface current, and silicate had < 0.5 % contribution to the models and were thus excluded from the kelp biome model.

Modelling

The Maximum Entropy (MaxEnt) modelling software has been widely applied for marine species distribution modelling with presence-only data (e.g., Tittensor et al. 2009; Verbruggen et al. 2009; Yesson et al. 2012; Basher et al. 2014a; Saeedi et al. 2016; Jayathilake and Costello 2018; Martinez et al. 2018). We used MaxEnt version 3.3.3k (Phillips et al. 2006; Phillips and Dudik 2008) to generate the kelp distribution model. In the current study, the model had 10 replicate runs with cross-validation, a maximum number of background points 10,000, and maximum iterations 1,000. The 'remove duplicate presence records' option was activated to keep one observation point per 30 arc sec grid cell. Separate MaxEnt models for species, genera, families and the order were created, and the environmental variables contributing most to the models tabulated. However, 25 species had insufficient occurrence records to develop individual MaxEnt models to predict their distributions.

By applying the model to all species together we were able to include records of even rare species. We previously found that this approach provides a more accurate model of a marine biome distribution (Jayathilake and Costello 2018). While our model used 13 potentially related variables, we also generated results (see model evaluation below) to determine the contribution of each variable individually.

Model evaluation

The accuracy of the MaxEnt model was evaluated using the receiver operating characteristic (ROC) curve and AUC (area under the ROC) (Peterson et al. 2008; Peterson et al. 2011). The ROC curve and AUC evaluate how well a species distribution model fits true presence and absence data (Elith et al. 2006; Elith et al. 2011). It is a graphical interpretation of the omission and commission rates. The omission rate is defined as the proportion of known occurrence records which are not predicted as presence. The proportion of known presence records predicted as present in the model is known as its sensitivity (1 - omission rate) (Phillips et al. 2004). Theoretically, the commission rate is the proportion of absences predicted as presence. The commission rate is defined as 1 – specificity, where specificity is the proportion of absences correctly predicted (Phillips et al. 2004). In a study where only presence data are available (i.e., no true absence data), MaxEnt selects random background points as pseudo-absences instead of true absence records (Phillips and Dudik 2008). Here it assumes that, all the grid cells without occurrence localities could be pseudo absences even if they have suitable environmental conditions (Phillips et al. 2004; Phillips et al. 2006). The current study area was ten times deeper than the average depth of kelp. This greatly increased the likelihood that the location that would be selected as a pseudo-absence would be a true absence.

MaxEnt has a high predictive performance with presence-only data (Elith et al. 2006). AUC is an indicator of the predictive power of a probabilistic model and ranges from 0 to 1, where the highest ranking is 1 (Phillips et al. 2004; Phillips and Dudik 2008; Peterson et al. 2008). The MaxEnt model indicates which variables best explained the distribution of the species using analyses of percent contribution, response curves, and a jack-knife test. While the MaxEnt model is being run the percentage contribution of each variable to the model is calculated. This gives a heuristic estimate of the relative contribution of the environmental variable to the MaxEnt model (Phillips 2017). The jack-knife test creates three plots to show how each variable has contributed to model training, model testing and the AUC. By evaluating the overall results of each jack-knife plot we can predict which of the variables mattered the most in determining an environmental or geographic distribution.

The post image processing of the MaxEnt modelled map used ArcGIS version 10.5.1. The MaxEnt probability values above 0.45 gave the most visibly similar geographic coverage to the field observation records. Those areas were considered to define the global distribution of the kelp biome. The accuracy of the classified map was cross-checked with another separate dataset of the order Laminariales downloaded from the GBIF (from 2018 to 2020) (Jayathilake and Costello 2020b). The MaxEnt probability values for occurrence records were extracted using the ArcGIS tool "raster value to point". The percentage of the occurrence records plotted within the predicted area were calculated using the MaxEnt probability values of these new occurrence records. MaxEnt probability values of these records were given in the last column of the table available in Jayathilake and Costello (2020b). The original abiotic layers were on the WGS84 geographical coordinate system. Thus, the initial MaxEnt modelled map used WGS84 geographical coordinate system which has larger grid cells at lower latitudes. We converted the MaxEnt modelled map to cylindrical equal-area projection (all grid cells have the same area) using the ArcGIS projection tool to calculate the true area of distribution and the coastline length covered by the kelp biome.

Results

At the order level, the laminarian kelp biome data contained 44,265 occurrence records distributed mainly in temperate and sub-Polar Regions. There were no occurrence records from the tropics and Antarctica (Fig. 1).

The modelled kelp biome map closely matched the distribution of reported occurrence records (Fig. 1 and 2). The high AUC indicated that the model had a probability of 0.771 to discriminate predicted presence records over the pseudo-absence records. In the validation dataset 86% (2,626 out of 3,054 occurrence records from 2018 to 2020) were plotted within the area predicted by a MaxEnt probability value of ≥ 0.45 and the remaining area at a spatial resolution of 30 arcsec (Fig. 3).

The biome covered 1,469,900 km^2 and 22 % of the world's coastline. The modelled map predicted the distribution of kelp mainly in the temperate, sub-Polar and the Arctic Ocean. The model predicted locations suitable for kelp which lacked georeferenced records in GBIF and OBIS, namely: the Atlantic coast of Argentina; Hokkaido Island, Japan; Shandong Peninsula, China; and Svalbard Island in the Arctic Ocean. However, the model did not predict laminarian kelp forests in the tropics and Antarctica.

The annual average sea surface temperatures (SST), distance from land, the maximum sea surface temperature and wave height, were the topmost variables contributing to the MaxEnt model (Table 2). The environmental variable with the highest gain when used in isolation was the annual average SST. Thus, the average SST had the most useful information by itself. Distance from the land was the third, wave height was the fourth, and dissolved oxygen the fifth most important variable for predicting the distribution of kelp (Table 2).

The probability of occurrence of kelp decreased with depth from 0 to 100 m, and no kelp occurred deeper than 250 m (Fig. 4). Most kelp occurred within 1 km of land. Kelp largely occurred with a maximum SST from 7 ºC to 27 ºC, and average from 5 ºC to 25 ºC. Kelp never occurred above an annual maximum of 30 ºC and an annual average of 27 ºC. The probability of kelp occurrence increased with wave height up to 7 m. Although no kelp was predicted above a salinity of 37.5, there were peaks of occurrence at 5 and 35 PSS (Fig. 4). The low salinity peak was due to the presence of *Chorda filum* in the Baltic Sea, parts of which have low salinity. Note that this species has recently been moved into a new order outside Laminariales (Stark et al. 2019).

The results from the training gain, test gain, and AUC jack-knife test plots showed a similar pattern of the contribution of each variable for the model. The average and maximum SST gave higher regularized training, test gain, and AUC compared to other variables (Fig. 5). The next most important variables were dissolved oxygen, wave height and the distance from land. If MaxEnt used only slope, salinity and pH, there was almost no gain in all three plots (Fig. 5). Thus, these three variables were not meaningful for predicting the global distribution of kelp.

Of the 70 species used in this study for which geographic coordinates were available, 46 species had insufficient georeferenced records to be successfully modelled. Wave height was the topmost for 23, and one of the top three most important environmental variables for 35 of these species in the MaxEnt models (Table 3). Distance from the land was the next most important variable, being amongst the top three variables for 21 species, followed by minimum SST (14 species). Wave height and land distance, followed by minimum and average SST, were also the most important variables at the genus level (Table 4). Wave height, average SST and minimum SST were the most important variables at the family level (Table 5).

Discussion

In this study, we provide the first global distribution map of laminarian kelp as a polygon layer that can be used in geographical information systems (GIS). This polygon layer has a more complete geographical distribution of the kelp biome than the published range maps of kelp species. However, the map had a very similar distribution to the observed field records (Fig. 1), and as reported in the literature (Steneck et al. 2002; Wernberg et al. 2019; Wernberg and Filbee-Dexter 2019).

Our model predicted that kelp was limited to latitudes 25° to 70° in the northern, and 25° to 55° in the southern, hemispheres. Of 3,000 newly recorded occurrences from 2018 to 2020 86% were plotted on the biome and 14% were plotted nearby (Figures 2 and 3). Such variability is to be expected considering both the spatial resolution of the coastline and environmental data, and variance in reporting latitude and longitude coordinates.

Kelp occupied 1,469,900 km^2 and 22 % of the world's coastline. Previous studies estimated that 25% of the world's coastline was covered by kelp forests (Filbee-Dexter and Wernberg 2018; Wernberg et al. 2019). Thus, the kelp biome is the second most widely distributed marine biome, following seagrass with 1,646,788 km^2 (Jayathilake and Costello 2018). Following the usage in terrestrial ecology, equivalent marine biomes are large areas characterised by plants of similar life-form that provide enduring three-dimensional habitat for other species (Costello et al. 2020). The other marine biomes have ten times less area than kelp, namely zooxanthellate coral with 151,390 km^2 (UNEP-WCMC 2018), and mangroves with 136,850 km^2 (Giri et al. 2011).

Some of the locations predicted to contain kelp in our map, but without occurrence records in GBIF and OBIS, were reported to have kelp forests in the literature. *Macrocystis pyrifera* and *Undaria pinnatifida* have been recorded in the Gulf of Nuevo, along the coast of Argentina from Puerto Deseado (Santa Cruz province) to Mar del Plata (Buenos Aires province) (Raffo et al. 2009; Pereyra et al. 2017; Paula et al. 2018). *Laminaria japonica* and *Saccharina japonica* occur along the coast of Shandong Peninsula, China (Wu et al. 2016; Shao et al. 2019). *Laminaria japonica, L. religiosa* and *U. pinnatifida* occur around Hokkaido Island, Japan (Matsunaga et al. 1999). *Alaria esculenta, Laminaria digitata*, and *Saccharina latissimi* occur in Hornsund, and *L. digitata* in Kongsfjorden, Svalbard (Włodarska-Kowalczuk et al. 2009; Bartsch et al. 2016). The current map did not predict any suitable locations in Antarctica and no laminarian kelp have been reported there (Moe and Silva 1977; Quartino and Boraso de Zaixso 2008; Wernberg et al. 2019). This suggests that the absence of laminarian kelp in these regions is primarily due to environmental unsuitability. Thus, our map appears to be an accurate representation of the kelp biome on a global scale. However, the tropical deep-water kelp distributions were not predicted in this model due to a lack of occurrence records from the tropics and because the mean sea bottom temperature variable was excluded from the analysis due to its poor contribution to the model. These communities should be modelled separately with deep water variables.

As a photosynthetic plant, kelp is limited to the photic zone. In this study, the MaxEntprobability of the presence of kelp was high between 0 to 100 m depth, and it was limited to 1 km from the land (Fig.4). However, it is likely that there may be offshore rocky reefs, such as the tops of seamounts, where kelp may occur but were not detected due to the spatial resolution of our data (Parker and Tunnicliffe 1994; Bo et al. 2011). Kelp forests always occur on hard substrata such as rocky seabeds (Teagle et al. 2017, Wernberg et al. 2019). The present study could not include seabed substrata because a global layer is not available. Nevertheless, the accuracy of the map suggests that sufficient rocky substrata exist for all regions where temperature and light are suitable. However, more detailed regional maps of kelp distribution would benefit from including seabed substratum within the present biome map.

Kelp had an increased probability of presence with increasing wave height from 1 m to 7 m, with a low probability of occurrence in areas without wave action (Fig.4). Most kelp species prefer turbulent water (Hurd 2000, Wernberg et al. 2019). For the individual species, genera and families, wave height was generally the most important factor in influencing their distribution. Species such as *Laminaria hyperborea* and *Alaria esculenta* are more common on wave exposed coasts (Frid and Kitching 1988; Norton 1992; Kraan et al. 2000; Pedersen et al. 2012).

We confirmed that the annual average sea surface temperature is the most significant factor limiting the distribution of the kelp biome, as suggested by others (e.g., Lüning 1990; Muller et al. 2009). Kelp occurred in average sea surface temperatures from 5 ºC to 25 ºC and was rare above 27 ºC (Table 2). Thus, if sea surface temperature increases beyond these temperatures, such as due to global warming, it will alter the kelp distribution (Martinez et al. 2018; Assis et al. 2016). Indeed, the range of Australian temperate kelp forests has contracted after ocean warming and extreme heat waves (Wernberg et al. 2012; Wernberg et al. 2016). *Macrocystis pyrifera* forests in Australia have been predicted to disappear if the predicted high sea surface temperatures in 2100 eventuate (Wernberg et al. 2011; Martínez et al. 2018). In contrast, Arctic kelp forests of *Laminaria digitata* have extended with ocean warming into areas that were previously too-cold (Bartsch et al. 2016). However, increases in UV radiation, sediment loading and freshwater inputs can also negatively impact the distribution of the Arctic kelp communities (Filbee-Dexter et al. 2019). Modelling of the future kelp biome distribution is necessary to predict its responses to climate change.

The kelp biome map indicates where kelp forests could occur. If kelp is absent, it may be due to ocean warming, high turbidity, and/or over-grazing following 'trophic cascades' caused by hunting and fishing of animals that predate sea urchins, and consequent over-grazing of kelp by the sea urchins (e.g., Leleu et al. 2012; Filbee-Dexter and Scheibling 2014). Future studies may model the potential distribution of individual kelp species at local and regional scales, so as to provide finer spatial resolution for local scale conservation and fishery management. The availability of additional data for the species with insufficient data may allow their range to be mapped. The present map may also be a useful data layer for predicting the occurrence of kelp-associated species and estimating 'blue carbon' budgets. Moreover, knowing the global extent of the kelp biome is important for the conservation of not only kelp but associated species, including species threatened with extinction or important to fisheries. Thus, the present kelp biome area was included as one of the biodiversity layers in designing a global network of Marine Protected Areas (Zhao et al. 2020).

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Table 1. List of laminarian kelp species and species names used in this study to model the global distribution of the kelp biome.

Agaraceae

Agarum clathratum Dumortier, 1822
Agarum turneri Postels & Ruprecht, 1840
Neoagarum fimbriatum (Harvey) H.Kawai & T.Hanyuda, 2017
Costaria costata (C. Agardh) De A. Saunders, 1895
Dictyoneurum californicum Ruprecht, 1852
Dictyoneurum reticulatum (De A.Saunders) P.C.Silva, 2008
Thalassiophyllum clathrus (S. G. Gmelin) Postels & Ruprecht, 184

Alariaceae

Alaria angusta Kjellman, 1889
Alaria crassifolia Kjellman, 1885
Alaria crispa Kjellman, 1889
Alaria esculenta (Linnaeus) Greville, 1830
Alaria marginata Postels & Ruprecht, 1840
Alaria praelonga Kjellman, 1889
Alaria pylaii (Bory de Saint-Vincent) Greville, 1830
Eualaria fistulosa (Postels & Ruprecht) M. J. Wynne, 2009
Lessoniopsis littoralis (Farlow & Setchell ex Tilden) Reinke, 1903
Pleurophycus gardneri Setchell & Saunders ex Tilden, 1900
Pterygophora californica Ruprecht, 1852
Undaria pinnatifida (Harvey) Suringar, 1873

Chordaceae

Chorda filum (Linnaeus) Stackhouse*, 1797***

Laminariaceae

Cymathaere triplicata (Postels & Ruprecht) J.Agardh, 1868
Hedophyllum bongardianum (Postels & Ruprecht) Yendo, 1914
Hedophyllum dentigerum (Kjellman) Starko, S.C.Lindstrom & Martone, 2019
Hedophyllum sessile (C.Agardh) Setchell, 1901
Laminaria abyssalis A.B.Joly & E.C.Oliveira, 1967
Laminaria brasiliensis A.B.Joly & E.C.Oliveira, 1967*
Laminaria digitata (Hudson) J.V.Lamouroux, 1813
Laminaria ephemera Setchell, 1901
Laminaria farlowii Setchell, 1893
Laminaria hyperborea (Gunnerus) Foslie, 1884
Laminaria longipes Bory de Saint-Vincent, 1826
Laminaria ochroleuca Bachelot de la Pylaie, 1824
Laminaria pallida Greville, 1848
Laminaria rodriguezii Bornet, 1888
Laminaria setchellii P.C.Silva, 1957
Laminaria sinclairii (Harvey ex J.D.Hooker & Harvey) Farlow, Anderson & Eaton, 1878
Laminaria solidungula J.Agardh, 1868
Laminaria yezoensis Miyabe, 1902
*Macrocystis pyrifera (*Linnaeus) C. Agardh, 1820
Nereocystis luetkeana (K. Mertens) Postels & Ruprecht, 1840
Pelagophycus porra (Léman) Setchell, 1908
Postelsia palmaeformis Ruprecht, 1852
Saccharina angustata (Kjellman) C.E.Lane, C.Mayes, Druehl & G.W.Saunders, 2006
Saccharina cichorioides (Miyabe) C.E.Lane, C.Mayes, Druehl & G.W.Saunders, 2006
Saccharina complanata (Setchell & N.L.Gardner) Gabrielson, Lindstrom & O'Kelly, 2012
Saccharina japonica (J.E. Areschoug) C.E.Lane, C.Mayes, Druehl & G.W.Saunders, 2006
Saccharina latissima (Linnaeus) C.E.Lane, C.Mayes, Druehl & G.W.Saunders, 2006
Saccharina longicruris (Bachelot de la Pylaie) Kuntze, 1891
Saccharina nigripes (J.Agardh) Lontin & G.W.Saunders, 2015
Streptophyllopsis kuroshioense (Segawa) Kajimura, 1981

Lessoniaceae

Ecklonia biruncinata (Bory) Papenfuss, 1944
Ecklonia brevipes J. Agardh, 1877
Ecklonia cava Kjellman, 1885
Ecklonia fastigiata (Endlicher & Diesing) Papenfuss, 1940
Ecklonia kurome Okamura, 1927
Ecklonia maxima (Osbeck) Papenfuss, 1940
Ecklonia muratii Feldmann
Ecklonia radiata (C. Agardh) J. Agardh, 1848
Ecklonia richardiana J. Agardh, 1848
Ecklonia stolonifera Okamura, 1913
Egregia menziesii (Turner) Areschoug, 1876
Eisenia cokeri M. Howe, 1914
Lessonia adamsiae C. H. Hay, 1987
Lessonia brevifolia J. Agardh, 1894
Lessonia corrugata Lucas, 1931
Lessonia flavicans Bory de Saint-Vincent, 1825
Lessonia nigrescens Bory de Saint-Vincent, 1826
Lessonia tholiformis C. H. Hay, 1989
Lessonia trabeculata Villouta & Santelices, 1986
Lessonia variegata J. Agardh, 1878

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* Marins et al. (2012) considered *L. brasiliensis* a synonym of *L. abyssalis. ** Chorda filum has since moved to another Order (ref* Starko et al. 2019)

Table 2. The environmental variables used in the Maxent models to predict the geographic distribution of kelp species of the order Laminariales. Columns indicate the range of each variable in the data used, the range kelp occurred most frequently in, and statistics on the relative contribution of each variable used to predicted the distribution of kelp. SST = sea surface temperature. PSS = practical salinity scale units.

Abiotic variable	**Unit**	**Variable range**	**Most suitable range**	**Percent contribution**
Average SST	ºC	0-35	5-25	47.7
Land Distance	km	0-20	0-1	23.7
Maximum SST	ºC	0-35	7-27	15.9
Wave height	m	0-8	1-8	9.5
Dissolved Oxygen	ml l^{-1}	1-10	5-7	1.2
Depth	m	0-1000	0-100	0.7
Nitrate	µmol $^{-1}$	0-30	5-14	0.3
pH		6.6-8.6	7.9-8.3	0.3
Photosynthetically Active Radiation	Einstein/m^2/ day	0-55	25-40	0.3
Phosphate	µmol $^{-1}$	0-2.5	0.1-1.0	0.1
Salinity	PSS	0-45	0-5 and 30-37	0.1
Slope	degree	0-14	0-3	0.1
Diffuse Attenuation Coefficient	m^{-1}	0-65	0-25	0

Table 3. Estimates of relative contributions of the environmental variables to the MaxEnt model of the laminarian kelp species. SST = Sea Surface Temperature, SBT = Sea Bottom Temperature, DAC= Diffuse Attenuation Coefficient, PAR= Photosynthetically Active Radiation.

Species	**1st**	**2nd**	**3rd**
Agarum clathratum	Land distance	Wave height	Maximum SST
Agarum turneri	Depth	Phosphate	Wave height
Costaria costata	Wave height	Land distance	Salinity
Dictyoneuropsis reticulata	Wave height	Land distance	Minimum SST
Alaria crispa	Wave height	Phosphate	Land distance
Alaria esculenta	Wave height	Mean SBT	Nitrate
Alaria marginata	Wave height	Land distance	Minimum SST
Alaria praelonga	Wave height	Land distance	Phosphate
Eualaria fistulosa	Wave height	Land distance	Phosphate
Lessoniopsis littoralis	Wave height	Land distance	Salinity
Pleurophycus gardneri	Wave height	Land distance	Salinity
Pterygophora californica	Wave height	Minimum SST	Land distance
Undaria pinnatifida	Land distance	Wave height	Minimum SST
Chorda filum	Mean SBT	Wave height	Land distance
Laminaria abyssalis	Minimum SST	Wave height	Nitrate
Laminaria brasiliensis	Minimum SST	Dissolved Oxygen	Wave height
Laminaria digitata	Average SST	Wave height	Land distance
Laminaria ephemera	Wave height	Land distance	pH
Laminaria hyperborea	Wave height	Average SST	Minimum SST
Laminaria ochroleuca	Average SST	Nitrate	Phosphate
Laminaria pallida	PAR	Wave height	Maximum SST
Laminaria rodriguezii	Average SST	Minimum SST	Nitrate
Laminaria setchellii	Wave height	Land distance	Maximum SST
Laminaria sinclairii	Wave height	Maximum SST	Land distance
Laminaria solidungula	Depth	pH	Maximum SST
Laminaria yezoensis	Wave height	Phosphate	Land distance
Macrocystis pyrifera	Wave height	Land distance	Minimum SST
Nereocystis luetkeana	Wave height	Land distance	Minimum SST
Pelagophycus porra	Nitrate	Wave height	Slope
Postelsia palmaeformis	DAC	Wave height	Minimum SST
Saccharina dentigera	Wave height	Land distance	Nitrate
Saccharina latissima	Wave height	Average SST	Land distance
Saccharina sessilis	Wave height	Land distance	DAC
Ecklonia cava	Maximum SST	Phosphate	Wave height
Ecklonia kurome	Maximum SST	Depth	PAR
Ecklonia maxima	Wave height	PAR	Phosphate
Ecklonia radiate	Salinity	Wave height	Land distance
Egregia menziesii	Wave height	Land distance	Minimum SST
Lessonia corrugate	Wave height	Minimum SST	Land distance
Lessonia flavicans	Land distance	Phosphate	Dissolved Oxygen
Lessonia variegate	Minimum SST	Land distance	Nitrate

Table 4. Estimates of relative contributions of the environmental variables to the MaxEnt model of the laminarian kelp genera. SST = Sea Surface Temperature.

Genus	1st most contribution	2nd most contribution	3rd most contribution
Agarum	Wave height	Land distance	Salinity
Alaria	Average SST	Wave height	Land distance
Chorda	Average SST	Wave height	Land distance
Costaria	Wave height	Land distance	Salinity
Dictyoneuropsis	Wave height	Land distance	Minimum SST
Ecklonia	Minimum SST	Land distance	pH
Egregia	Wave height	Land distance	Diffuse Attenuation Coefficient
Laminaria	Average SST	Wave height	Land distance
Lessonia	Land distance	Minimum SST	Wave height
Macrocystis	Wave height	Land distance	Minimum SST
Nereocystis	Wave height	Land distance	Nitrate
Postelsia	Diffuse Attenuation Coefficient	Wave height	Minimum SST
Pterygophora	Wave height	Minimum SST	Diffuse Attenuation Coefficient
Saccharina	Wave height	Average SST	Land distance
Thalassiophyllum	Average SST	Phosphate	Minimum SST
Undaria	Land distance	Wave height	Average SST

Table 5. Estimates of the relative contributions of the environmental variables to the MaxEnt model of the laminarian kelp families. SST = Sea Surface Temperature.

Family	1st most contribution	2nd most contribution	3rd most contribution
Agaraceae	Wave height	Land distance	Average SST
Alariaceae	Wave height	Average SST	Land distance
Chordaceae	Average SST	Land distance	Wave height
Laminariaceae	Average SST	Wave height	Land distance
Lessoniaceae	Minimum SST	Land distance	Wave height

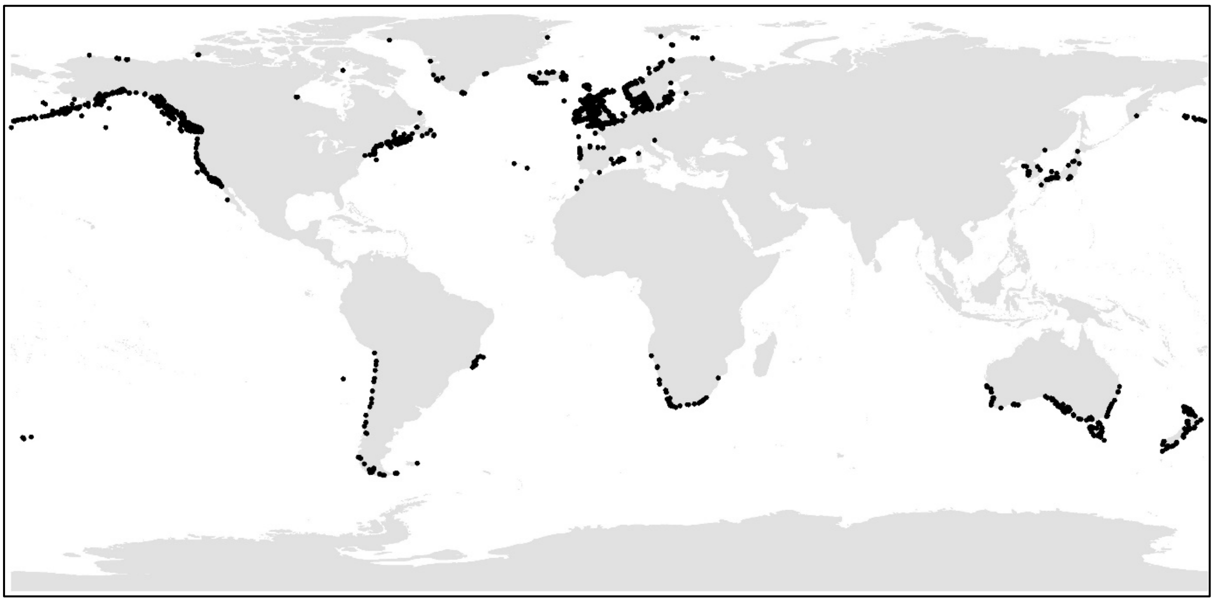

Figure 1. The distribution of laminarian kelp observations used in this study.

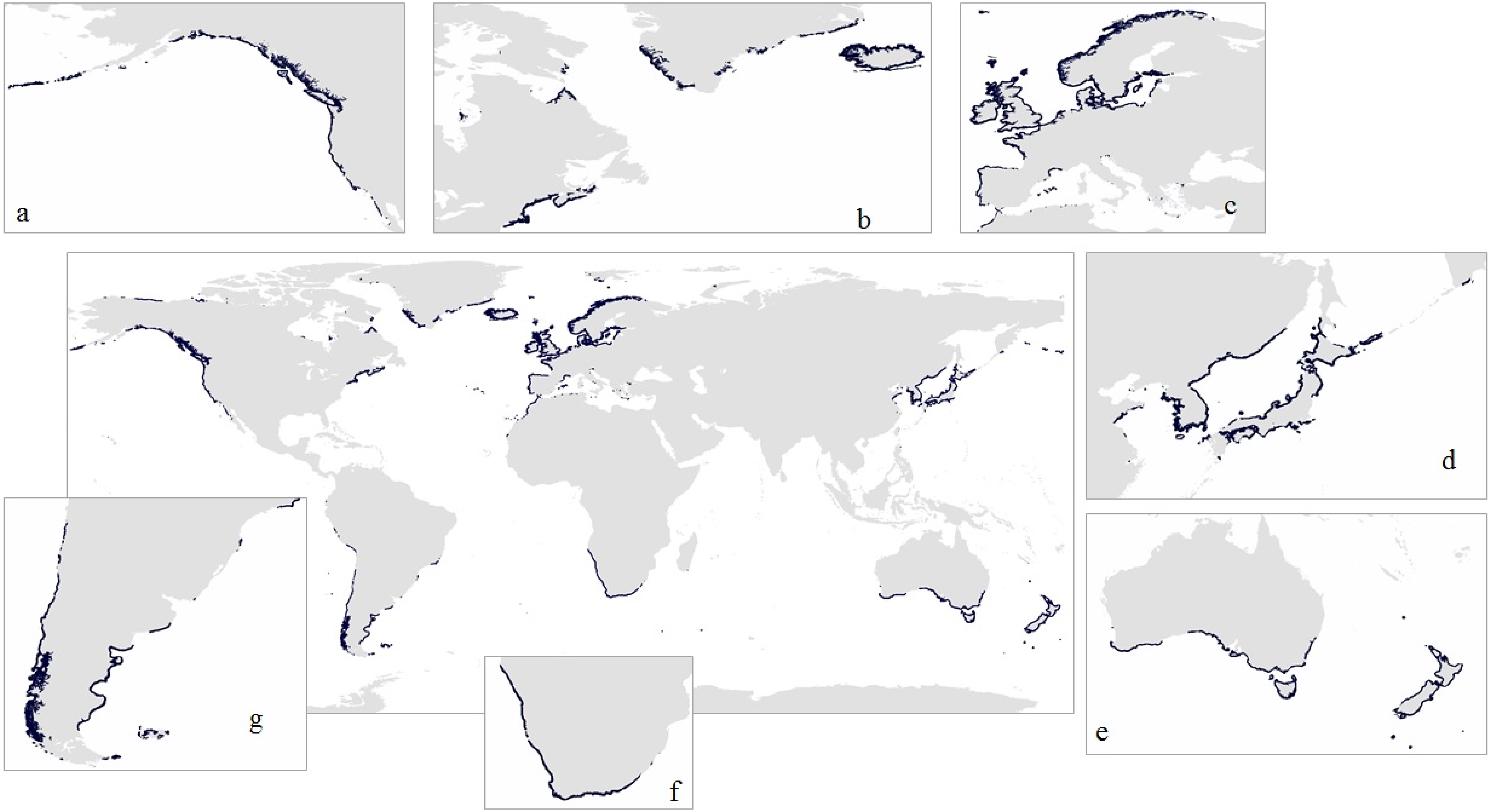

Figure 2. The predicted environmental range for the order Laminariales. The dark blue colour indicates the MaxEnt probability of distribution. (a) west coast of North America, (b) north-west Atlantic including Greenland and Iceland, (c) Europe, (d) north-west Pacific including parts of Japan, China, Russia, and Korea, (e) New Zealand and southern Australia, (f) southern Africa, (g) southern South America.

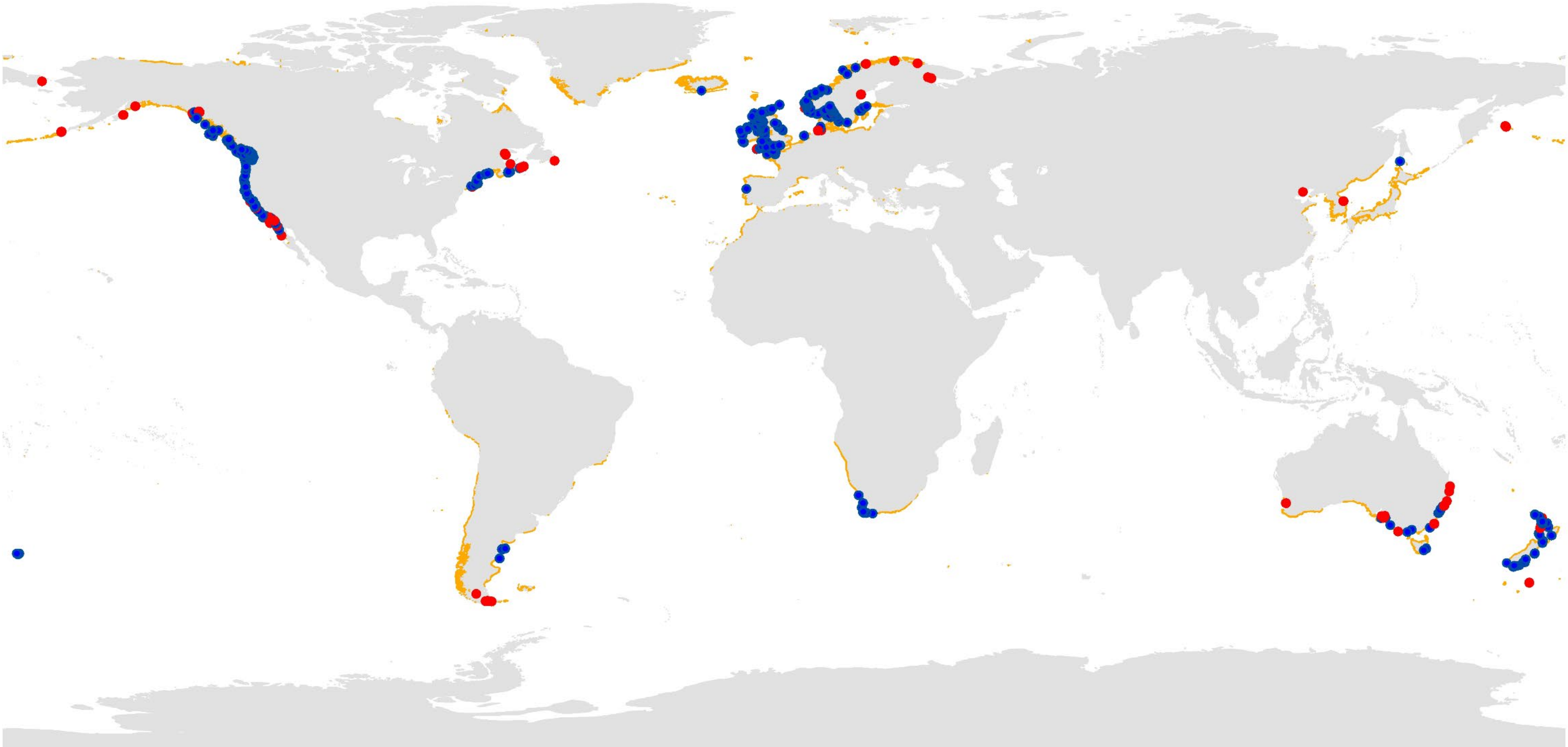

Figure 3. The comparison of the predicted laminarian kelp biome (yellow) to the occurrence of additional data published in since 2018 that were not used in modelling the biome; 86% of these new records occurred within the biome. The blue colour points indicate the occurrence records have >=0.45 maxent probability value (plotted within the predicted area) and the red colour points show the occurrence records have < 0.45 MaxEnt probability values (plotted out of the predicted area).

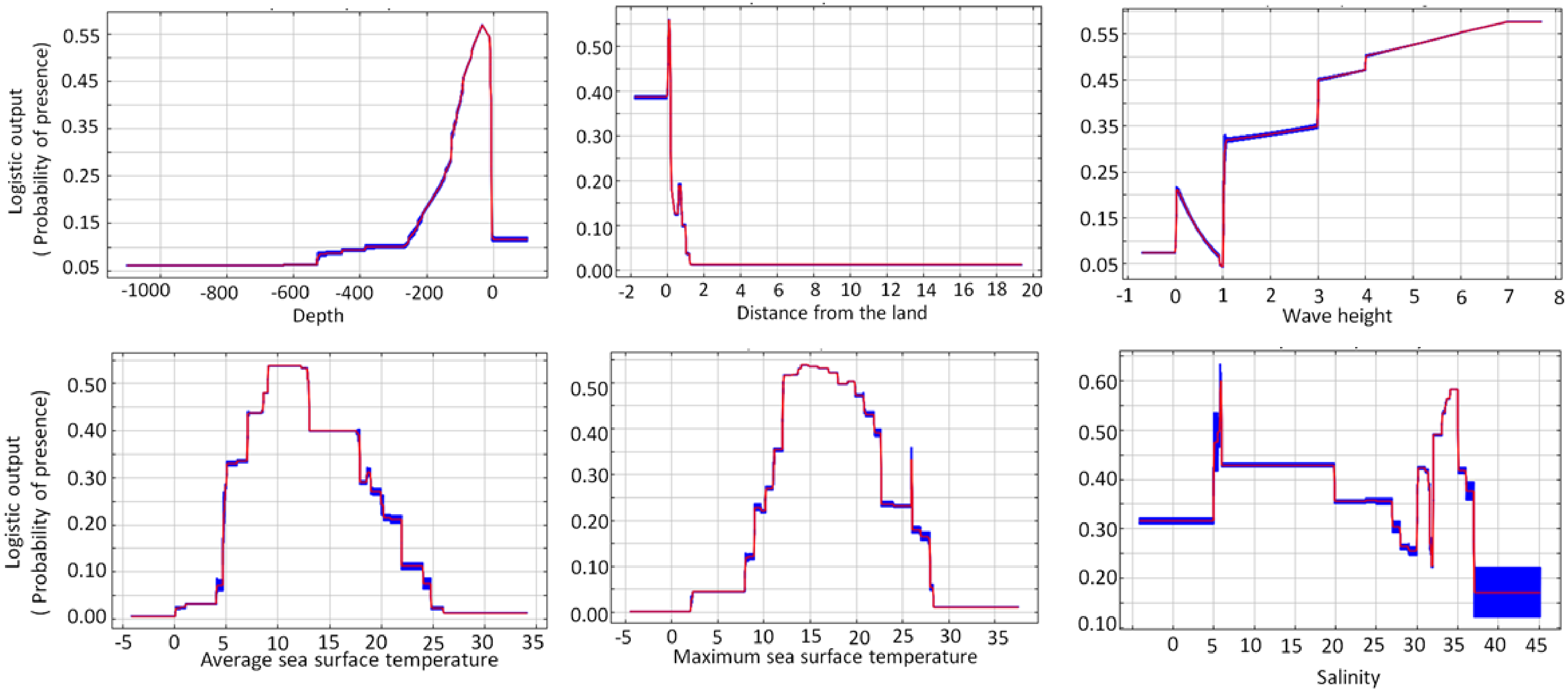

Figure 4. The response of kelp to depth, distance from land, wave height, average sea surface temperature, maximum sea surface temperature, and salinity.

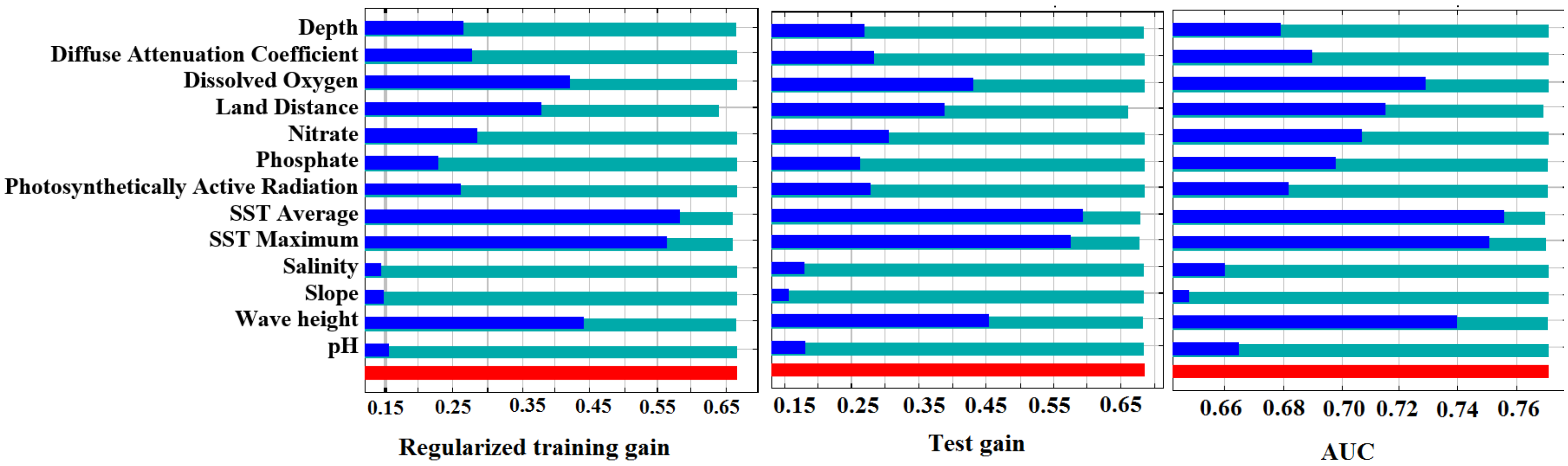

Figure 5. The results of the jack-knife tests of variable importance: (a) training gain; (b) test gain, (c) AUC. Jack-knife results were calculated without the variable (green), with only variable (blue) and with all variables (red).