MODELLING DISTRIBUTION AND ASSOCIATED ENVIRONMENTAL PREFERENCES OF SOUTH AFRICAN KELPS AND THEIR CLOSE RELATIVES

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PLAGIARISM DECLARATION

I know the meaning of Plagiarism and declare that all of the work in the document, except

for that which is properly acknowledged, is my own.

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Abstract

Kelp are central components of marine ecosystems that are found on the west coast of South Africa and in temperate regions around the world. They are ecologically important in providing vertical habitats, and sustaining diverse life-forms. The kelp species that are investigated in this study are *Ecklonia cava, Ecklonia maxima, Ecklonia radiata, Laminaria pallida* and *Laminaria ochroleuca. Ecklonia maxima, E. radiata* and *L. pallida* are dominant South African kelps, therefore studying these species provides information about their distributions and environmental preferences. *E. cava* and *L. ochloleuca* are of interest as they are close relatives to South African kelp species, and add to the understanding of *Ecklonia* and *Laminaria* in a more global context. The aims of this study were to map the biogeographical distribution of each species, and model their potential niches based on the environmental conditions that facilitate their growth. Species Distribution Modelling was used to map the fundamental niche of each species. The Maxent method was used to model predictive niches by layering known coordinates of where each species is found, along with the Bio-ORACLE dataset of 23 environmental variables, consisting of satellite and *in situ* data. The Carto cloud computing platform was used to map the current distribution of each species. The major environmental predictors of each species distribution were identified in the modelling process and contributed to the final predicted habitat suitability maps. The results of this study show that Maxent identified maximum, minimum, mean and range in sea surface temperature to be associated with all species' distribution. Measures of irradiance or light availability (specifically Photosynthetically Active Radiation, Diffuse Attenuation and cloud cover), were important predictors of four of the species' distributions. Chlorophyll, a proxy for nutrients, emerged as an important correlate of most distributions, whilst silicate, phosphate and calcite were important, particularly to the distribution of kelp species found outside of South Africa. There were regions identified

where each species could potentially grow, but are not found. The results show that while *E. maxima* and *L. pallida* are distributed along the west coast of Southern Africa, *L. pallida* could potentially grow along the west coast of South America, whilst *E. maxima* appears to have a niche endemic to South Africa. *Ecklonia radiata* is distributed along the south coast of South Africa as well as southern Australia, New Zealand, whilst it could potentially grow in the north Atlantic, northeast Pacific and southeast Pacific. *Ecklonia cava* is only found on the Japanese and South Korean coast and is predicted to be able to spread down the coast of China. *Laminaria ochroleuca* is distributed along the coasts of Spain, Portugal, France and Northern Africa with a widespread distribution on the British coastline, with a predicted potential to extend to western Ireland. Other suitable habitats for *L. ochroleuca* were southern Australia and New Zealand. *Ecklonia maxima* and *L. pallida* have overlapping distributions, whilst all other species have different distributions. The ecological preferences of each of these species differed in parameter, but were related to the same variables; temperature, light and nutrients. The South African species, *E. maxima, E. radiata* and *L. pallida,* differed in their preferences, including those occupying the same coastline. All species of kelp had variably unique distributions and varying environmental preferences compared to their congenerics. The possible causes for species not being able to grow in identified niches are likely to be temperature limits, light and nutrient limits, physical barriers and limitations to movement and establishment, as well as geographical and associated evolutionary adaptations that may limit dispersal. Besides the environmental variables analysed, biological, oceanographic and *in situ* data is deemed important in gaining a complete and causal understanding of species distributions and their drivers. This study provides insight into South African kelp systems and their close relatives in a global context, and shows the successful use of niche modelling methods that can be more widely applied in marine research, conservation and management.

Chapter 1: Introduction

Oceans and global change

The oceans cover over 70% of the Earth's surface and have played a vital role in the evolution of the planet's climate (Brierley et al. 2009). Since 1960, the ocean's net heat uptake has been found to be around 20 times more than the atmosphere, whilst ocean temperatures have warmed by 0.1°C from the surface to 700m depth from 1960 to 2003 (Bindoff et al. 2007). This is one effect of global climate change, which is one of the most prevalent human transformations of the Earth, representing a great threat to ecological functioning and ecosystem services (Rosenzweig et al. 2007). The marine environment provides >60% of the value of ecosystem services occurring in nature (Costanza et al. 1997). However, human activities are impacting the environment, through increased industrialisation and carbon emissions that have been found to contribute to global temperature increases, nutrient changes, sea level rise, altered regional weather patterns, ocean acidification, and altered ocean circulation (Brierley et al. 2009). Anthropogenic climate change has altered the biogeography of many marine species (Barton et al. 2016). Changes to a system are becoming more widely recognised to be a combination of discrete events, as well as continuous, gradual change, which may vary temporally and spatially (Wernberg et al. 2012). A single change in the environment could cause a species to become negatively affected, which subsequently impacts other organisms and processes that may depend on it. This cascading effect is known as a trophic cascade, which has the potential to impact ecosystem engineers and consequently alter an entire ecosystem. One such ecosystem engineer is large brown alga known as kelp, which forms the focus of this study.

Kelps and their importance

Large brown algae from the order Laminariales, more commonly referred to as kelps are biodiverse organisms that were first noted by Charles Darwin who visited Australia in 1836 (Hayman 2009). Macroalgal beds are a dominant feature of the ocean, distributed on sub- and intertidal rocky substrata in warm to cold temperate waters (Steneck and Johnson 2013) and Artic regions (Lüning 1990; Bolton 2010). Kelp beds have, however, also been observed in some regions near the tropics where there are suitable cool-water micro-habitats (Graham et al. 2007). Kelp forests create a complex 3-dimensional habitat and food source for a diversity of marine organisms (Lippert et al. 2001). The communities that inhabit kelp beds are known to have high levels of endemism and diversity (Wernberg et al. 2011). Kelp are also biogenic engineers and habitat modifiers in that they provide vertical habitats that play a role in altering the light environment (Dillehay et al. 2008), sedimentation (Wernberg et al. 2005), coastal primary production (Moy et al. 2008), carbon capture and organic input (Chung et al. 2013), and hydrodynamics (Cornell 2003) of the ecosystem. Kelps act as efficient carbon pumps that play an effective role in climate change mitigation (Duarte et al. 2013). Kelp forests have provided food, medicine, materials and aesthetic value since the earliest humans inhabited temperate coasts (Shiel et al. 2015), being harvested for alginates used in the pharmaceutical, textile, food and paper industries (Bartsch et al. 2008), animal feed, human food and biogas (Hughes et al. 2012) to name but a few. Kelps are therefore not only ecologically important, but have a high economic value in many regions, which will be discussed further in this section.

Increasing temperatures, driven by climate change processes, have been reported to present threats to kelp systems (Wernberg et al. 2010, 2011). This is of concern since a change to these kelps and their associated communities could have a negative impact on

the multitude of goods and services they provide. Climate change often manifests as species range changes, therefore it is important to have a holistic understanding of kelps and their life histories, phylogenetics, evolution, physiological tolerances and biogeographical distributions. These five areas will be covered in this section to set the scene for this study.

Kelp life history considerations

All Laminariales have heteromorphic life histories in which a large macroscopic sporophyte alternates with a microscopic filamentous gametophyte (Mohring et al. 2013), where each life history phase may respond differently to environmental stressors (Bartsch et al. 2008). Restrictions to kelp reproduction, recruitment and growth are imposed by high temperature limits or low survival limits, with the latter being particularly sensitive in the macroscopic life history phase (Lüning 1990). These limits are largely defined by temperatures, where elevated temperatures pose threats to survival (Wernberg et al. 2010). Reproduction and recruitment usually are limited by lower temperatures than the upper limit for adult survival (Mohring et al. 2013) whereas growth and productivity have been shown to be adversely affected at high temperatures (Hargrave et al. 2017). Environmental conditions can affect any stage in the recruitment cycle whether it is spore release, dispersal or settlement, or gamete release, dispersal and egg production (Sjøtun et al. 2006). Between reproductive stages the phenomena known as reproductive synchrony is linked to the timing of optimal environmental conditions (Mohring et al. 2013). Besides reproductive, recruitment and growth limits of kelp, lethal limits also exist. Lethal limits are conditions if which exceeded, can cause denaturation of proteins and damage to membranes, often resulting in algal death (Lüning 1990). Lethal limits, however, do not necessarily correlate with distributional limits of species with a heteromorphic life history (Lüning 1990). Gametophytes and young sporophytes are critical life history stages for the maintenance of kelp populations, where

differing light conditions are further determinants of survival and growth of the various developmental stages (Altamirano et al. 2004).

Kelp classification and phylogenetics

There are two genera that are investigated in this study. The genus *Ecklonia* (Arthrothamnaceae) consists of 16 taxonomically recognised species found in both the Northern Hemisphere and Southern Hemisphere (Rothman et al. 2015). It should be noted that *Ecklonia* was recently transferred to the family Arthrothamnaceae by Jackson et al. (2016). The genus *Laminaria* (Phaeophyceae) is a widely distributed genus with most species in the Northern Hemisphere and two species in the Southern Hemisphere (*Laminaria abyssalis* A.B.Joly & E.C.Oliveira and *Laminaria pallida* Greville) (Rothman et al. 2017). This study focuses specifically on three South African kelp species, *Ecklonia maxima* (Osbeck) Papenfuss*, Ecklonia radiata* (C.Agardh) J.Agardh and *L. pallida*, which are abundant and important species in South Africa, and their closest relatives *Ecklonia cava* Kjellman and *Laminaria ochroleuca* Bachelot de la Pylaie (Rothman et al. 2015).

A molecular study of *L. pallida* was undertaken by Rothman et al. (2017), which highlights the two variations of *L. pallida*, including the former *Laminaria schinzii* Foslie that was previously believed to be a different species*.* Both forms are morphologically variable along the Southern African west coast, *L. pallida* having a solid stipe form with the stipe widest near the holdfast, and *Laminaria schinzii* having a longer, hollow stipe that is wider in the middle, narrowing toward the ends. Rothman et al. (2017) confirmed that the *L. pallida* of Southern Africa, is a single species with its closest relative (sister species) being the northern Atlantic *L. ochroleuca*.

Bolton and Anderson (1994) observed that *E. radiata*, *E. cava* and *E. kurome* Okamura were difficult to tell apart by morphology. Rothman et al. (2015) confirmed by molecular data that *E. maxima* and *E. radiata* are indeed two distinct, though closely-related species in South Africa. Furthermore, morphological variance has been long known, a key observation being that *E. maxima* has a hollow stipe whilst *E. radiata* has a solid stipe (Lüning 1990). Rothman et al. (2015) also found that the East Asiatic species *E. cava* and *E. kurome* are in a distinct lineage separate from the Southern Hemisphere clade. *E. cava* was found to form a clade separate from *E. kurome,* however, it was not statistically supported (Rothman et al. 2015). Okamura (1927) had already noted that there was some difficulty in distinguishing between *E. cava* and *E. kurome*, stating that the central rachis of *E. kurome* varied while that of *E. cava* did not, and that the former was palatable while the latter was not. With these being the only differences, with little to no difference in morphology or genetics, as well as overlapping distributions, this study considers *E. cava* and *E. kurome* together, and refers to the North west Pacific distribution as being associated with *E. cava.*

Three guilds of kelp

There are three 'guilds' of kelp explained by Dayton (1985). The first of these guilds is the largest, forming floating canopies and include kelp such as *Macrocystis* C.Agardh, which may grow to 45m in length (Abbot and Hollenberg 1976). These kelp dominate kelp forests along the west coast of North and South America and are scattered around the Atlantic and Pacific oceans, including South Africa, southern Australia, New Zealand and the subantarctic islands. The second guild comprises smaller canopy forming kelps such as *E. maxima*, which are only found in the Southern Hemisphere on the west coast of South Africa. The third guild comprises species possessing stipitate kelp fronds, such as *L. ochroleuca* in Europe and the north west Pacific, as well as *E. radiata* in southern Australia and New Zealand, and

Japanese kelps in the northern Pacific. Most of these species are less than 5m in length although a few species may grow to 10m (Schiel and Foster 2015).

Evolutionary history and biogeography of kelps

It is suggested that members of the Laminariales had their origin in the Northern Hemisphere (Estes and Steinberg 1988) and crossed the tropics (Lüning 1990) to evolve into species that are better adapted to new environments in the Southern Hemisphere. The majority of the ancestral Laminariales are still known to occur on the island of Hokkaido (Kawai 1986), which suggests that the origins of the Laminariales were in fact in cold-temperate regions of the Northwest Pacific.

Lüning (1990) hypothesized that the genus *Laminaria* originated in the Northern Pacific based on the close relationship between northern Atlantic species of *Laminaria* that are the only species to have discoid holdfasts. Following this, he hypothesized a migration event via the Bering Strait to the Arctic and Northern Atlantic, with further migration across the equator to the south Atlantic, during a glaciation event, causing the colonization of South Africa (*L. pallida*) and Brazil (*Laminaria abyssalis*). Lüning (1990) suggested that *L. pallida* evolved from *L. ochroleuca* after hybridization experiments between the two species yielded evidence. This finding was supported by Rothman et al. (2017) who proved, using molecular sequencing, that *L. ochroleuca* and the two southern Atlantic species (*L. pallida* and *Laminaria abyssalis*) are in the same clade, with the sister relationship of this clade to the rest of the (ancestral) northern Atlantic species from the genus. The phylogenies further revealed a close relationship between the Northern Atlantic *L. digitata/L. hyperborea* (cold temperate) and the *L. abyssalis* (Hudson) J.C. Lamouroux /*L. pallida/L. ochroleuca* (warm temperate) clades.

The geographic distributions of *E. maxima* and *E. radiata* differ in that the former occupies the South African west coast, whilst the latter occurs in the south and east coast of South Africa. The evolution of *E. maxima* is hypothesized to be a result of an adaptation to the west coast cool, nutrient-enriched upwelling system: ie. the two *Ecklonia* species present in Southern Africa originated from an Australian *Ecklonia radiata* migrant (Rothman et al. 2015). Historically warmer conditions (3.5 Ma) may have allowed the migration of *E. radiata* westward from Australia whilst 2.5 Ma cooling, due to intensified upwelling, may have caused temperature drops below 20°C (Marlow et al. 2000). The population of *E. radiata* on the west coast is hypothesized to have developed a longer stipe, among other morphological adaptations to the high nutrient environment of the upwelling system and could have evolved into a different species, *E. maxima,* whilst on the east coast (with no new selection pressures) *E. radiata* may have remained (Rothman et al. 2015).

The well-known globally distributed kelp, *Macrocystis,* occurs in temperate regions including western North America, the Northern Hemisphere and the Southern Hemisphere and is a good colonizer which is important to its geographical dispersal. Understanding this widespread global kelp is crucial to providing context for the kelps in this study, particularly in relation to their potential to occupy specific niches. There are various hypotheses surrounding the origin of *Macrocystis.* The first is based on a Northern Hemisphere origin, based on biogeographic, paleoclimatic and fossil records (Lüning 1990). North (1986) however suggested that a Southern Hemisphere origin is likely due to the more widespread distribution in the Southern Hemisphere. Sequences by Coyer et al. (2001) suggest a very recent dispersal of *Macrocystis* from the northern to the Southern Hemisphere, involving a recent breaching of the tropical barrier. Molecular sequencing of *Macrocystis* further

inferred a Northern Hemisphere to the Southern Hemisphere dispersal based on (1) paraphyletic relationship of Northern Hemisphere individuals relative to well-supported monophyletic origin of Southern Hemisphere individuals and (2) greater sequence diversity within Northern Hemisphere individuals (Coyer et al. 2001). After colonization of the coastal area of western South America, subsequent dispersal throughout the Southern Hemisphere is likely to have occurred via dislodged rafts of transported eastward by the Antarctic Currents (Coyer et al. 2001). Fossil evidence further indicates that kelps radiated from the north Pacific following the Middle (15 Ma) to Late Miocene (Estes and Steinberg 1988). In terms of abiotic drivers of distribution, *Macrocystis* individuals at the northern limit are more tolerant of low nitrate concentrations than individuals southern locations and populations at the southern edge of the distribution are more tolerant of high temperatures (North 1986).

Kelp species distributions and physiological tolerances

The order in which the species are presented is in alphabetical order, listing South African species of each respective genus first, followed by the closely-related species found in other regions of the world.

Ecklonia maxima

Ecklonia maxima is endemic to cool temperate Southern Africa where, until recently, it occurred from Cape Agulhas westwards to north of Lüderitz, Namibia (Stegenga et al. 1997), forming variably dense kelp beds in the shallow sublittoral of these regions. After about 70 years of unchanged distribution, *E. maxima* has extended its range 73 km east of its previous eastern limit at Cape Agulhas towards Koppie Alleen, De Hoop Nature Reserve (Bolton et al. 2012). The species has also been reported to occur on several islands in the

south Atlantic, Indian and Pacific oceans (Guiry and Guiry 2017). However, except for St. Paul Island, which has a number of other seaweed species in common with South Africa, these records should be treated as doubtful as they have not been verified (Papenfuss 1942; Rothman et al. 2015).

The west coast of Southern Africa has a unique set of environmental conditions that is ideal for kelp growth, largely owing to upwelling conditions. The region is characterised by mean inshore seawater temperatures ranging from 12-16°C , with the mean of the warmest month being 13-19°C and the mean of the coldest month recorded at 11-14°C (Bolton 1986). Cape Point and Cape Agulhas are close to the break between the effects of the warm Agulhas and cool Benguela currents, but cooler temperatures still characterise these regions (Teske et al. 2013). The warm temperate south coast has monthly maximum temperatures between 20 and 29°C (Smit et al. 2013) and minimum monthly means between 10 and 15°C (Teske et al. 2011). These temperatures characterise the environment and adaptations of Southern African kelp species, with *Ecklonia maxima* and *L. pallida* being more suited to the cooler west coast and southern west coast temperatures. The upwelling in these regions is a major determinant of light availability as measurements of irradiance have been recorded to be much lower during periods of aquiscence than in upwelling conditions (Anderson 1982). It is hypothesised that the eastward distribution of *E. maxima* may be limited by higher inshore water temperatures (Bolton et al. 2012). *Ecklonia maxima* sporophytes can grow up to 12 m long dominating shallow waters, forming kelp forests down to 5–10 m deep (Rothman et al. 2006). Northward along the west coast, *E. maxima* is gradually replaced by *L. pallida* (Rothman et al. 2015).

Ecklonia radiata

Ecklonia radiata is a widely distributed species of kelp in the Southern Hemisphere being confirmed to occur in South Africa, Australia and New Zealand (Rothman et al. 2015), and also reported from Madagascar, and in the Northern Hemisphere from Oman and the central eastern Atlantic Ocean (Mauritania, Senegal, the Canary and Cape Verde Islands) (Guiry and Guiry 2017). Its South African distribution is influenced by the warm Agulhas Current with an annual mean of 17-19°C (mean in warmest month: 19-21°C; mean in coldest month: 13-17°C) (Bolton and Anderson 1987). The southern Australian distribution of the species is known to be characterised by temperatures ranging from 14-19°C, however, in the cooler southeastern upwelling region of Australia, the temperatures are between 12 and 14°C (Womersley 1981). Following this latitudinal gradient, in the southeastern region of Australia, with the addition of Tasmania, temperatures are not likely to exceed 15°C (Edwards 1979). It can therefore be inferred that the temperatures in the Australian region are transitional between cold and warm temperate regimes. Furthermore, the species is found along the coast of New Zealand which differs in temperature; Northern New Zealand is warm temperate (12-20°C) whilst the southern part is cold temperate (6-14°C) (Lüning 1990).

Ecklonia radiata sporophytes are generally less than 1 m long in South Africa (Stegenga et al. 1997) while in some locations in Australasia they can reach 2 m in length (Wernberg et al. 2003). A major morphological difference that is commonly observed is that *E. maxima* has a hollow stipe whilst *E. radiata* sporophytes have solid stipes (Wernberg et al. 2003). In South Africa, *E. radiata* occurs inshore on the south coast of South Africa, from Koppie Alleen in the De Hoop Nature Reserve eastwards to Port Edward (Rothman et al. 2015). Its occurrence at Koppie Alleen now overlaps with that of *E. maxima*'s (Bolton et al. 2012).

In Australia, *E. radiata* is distributed around the western and southern to the eastern coasts, from Kalbarri and the Abrolhos Island on the west coast around southern Australia and Tasmania to Caloundra in Queensland (Wernberg et al. 2003). It is further distributed throughout New Zealand and on many New Zealand Islands (Three Kings Island, Stewart Island, Snares Island) (Guiry and Guiry 2017). Southern Australia is reported to have experienced some of the fastest increases in ocean temperatures globally. For example, in south-eastern Australia, strengthening of the East Australian Current has caused warming at a rate of 0.023°C /year, which is approximately four times the global ocean warming average (Ridgway 2007).

Ecklonia cava

Ecklonia cava is found along the temperate region of central to southern Japan (Kawashima 1993; Terawaki 1993) as well as regions of the South Korean coast (Choi et al. 2016). *Ecklonia cava* grows just under the low tide mark to approximately 30 m deep on rocky substrata (Okamura 1936; Iwahashi et al. 1979). Because of its economic and ecological importance in Japan, many studies of *E. cava* have been undertaken concerning the local distribution and population structure. Most of these studies have been restricted to the populations distributed along the cooler temperate region of Japan but there have been relatively few studies in warmer temperate regions (Serisawa et al. 2001). It is reported that the photosynthetic rate of bladelets of *E. cava* decreases when water temperature exceeds 20°C under light conditions under 50 micromoles $m^{-2}s^{-1}$, and the dark respiration rate increases with the temperature rise (Serisawa et al. 2004) It is anticipated that the net production of individual *E. cava* decreases with seawater temperature rise, therefore, the increase of the seawater temperature might influence the disappearance of the *E. cava* population in certain regions (Serisawa et al. 2004). It has been found that individuals in

warmer localities have shorter stipes while those in cooler localities have longer stipes (Serisawa 2004).

Laminaria pallida

Laminaria pallida is found on the west coast of South Africa and Namibia, and grows as an understory to *E. maxima* (Anderson et al. 2003). It is the dominant kelp at depths of 8-20m (Jarman and Carter 1981) and requires a suitable rocky substratum. One morphological variation of *L. pallida* was previously known as *Laminaria schinzii. A* hollow stipe was observed in *Laminaria schinzii*, compared to *L. pallida'*s solid stipe (Lüning 1990). As mentioned earlier, this latter taxon is now regarded as a taxonomic synonym of *L. pallida*, whose northern distributional limit was suggested to be decreasing water clarity (Jarman and Carter 1981). The geographic distribution of *Laminaria pallida* is largely determined by water temperature, which is demonstrated by its confinement to areas off the Southern African coast that are affected largely by cold upwelled water (Dieckmann 1978). On the Namibian coast, the temperature range is recorded to be 12-14.8°C in Lüderitz and 12-18.4°C in Swakopmund, (Molloy 1990). The cool temperate seawater regime brought about by the upwelling characterises the distribution in northern Namibia (Graham et al. 2007).

Laminaria ochroleuca

Laminaria ochroleuca extends towards the north Atlantic on the coasts of Britain (Parke et al. 1948) and on the south of Brittany (Pereira et al. 2011). The northern limit of its distribution coincides with the 10°C February isotherm (van den Hoek 1982). *Laminaria ochroleuca* is also found on the coasts of Portugal, Spain, France, and Morocco (Hargrave et al. 2017). The existence of *L. ochroleuca* in the southern Northeast Atlantic and its sister species, *L. pallida* in the Southeast Atlantic (Rothman et al. 2017) is an interesting

observation with respect to the evolution of Atlantic *Laminaria*, in both Hemispheres. Sporophyte growth is arrested at temperatures below 10°C (Izquierdo et al. 2002) and the species is susceptible to cold damage during low winter temperatures (Hargave et al. 2002). Optimal temperatures for *L. ochroleuca* is around 16°C (Biskupa et al. 2014). Physiological limitations and its restricted capability to acclimatize to high temperatures (Izquierdo et al. 2002) could affect its distribution.

Environmental drivers of kelp distribution

Biogeography is the study of patterns in geographic distributions of an organism or species that are caused by gradients in the physical environment (Smit et al. 2013). Each species investigated in this study has previously undergone physiological studies to some degree, to understand their environmental preferences, particularly those pertaining to temperature, light and nutrients, which are basic abiotic requirements (Bearham et al. 2013; Schiel et al. 2015). A number of studies demonstrate that kelp growth is driven by sea water temperature, whilst fewer cases report other factors such as light (e.g. Lüning 1990). Temperature distribution is a major factor controlling latitudinal distribution of marine algae (Yarish et al. 1986). Temperature affects reaction rates and therefore influences physiological processes such as photosynthesis, respiration and development in kelp (Rinde and Sjotun 2005). Temperature has been known to be one of the most important drivers of marine species distribution (Wernberg et al. 2011) and is commonly measured as Sea Surface Temperature (SST). Varying temperature limits, whether maximum or minimum growth, reproduction or lethal limits, are important for every life history stage of kelps (Breeman 1988). Temperature limits determine the hardiest life history stages as well as revealing

sensitive stages of kelp growth, reproduction and ultimately, survival. Temperature limits of a species therefore give rise to their distributions and range limits.

Associated with temperature is nutrients, a major determinant of kelp productivity, which is observed to have an inversely proportional relationship (Waldron and Probyn 1992). Gao et al (2017) considered factors playing a limiting role in the distribution of Laminariales and suggested that nutrient availability is of prime importance. Chlorophyll is a proxy for nutrients, representing the productivity of a system, ie. the amount of nutrients, where low chlorophyll levels suggest low phytoplankton levels and vice versa. Phosphate and nitrates are nutrients that promote the production of phytoplankton, which composes the base of the marine food web. Jackson (1977) reported that the pattern in temperate oceanic waters is for surface waters to be depleted of fixed nitrogen, phosphorus and silicon by phytoplankton growth in summer, and to be enriched during the winter by mixing with a high nutrient subsurface. Chlorophyll levels are further indication of light-harvesting phytoplankton which require these pigments for photosynthesis. Chlorophyll is therefore an indicator of productivity and is generally more abundant in cool waters in upwelling regions, with high nutrient content. Silicate is also one of the measures of productivity as phytoplankton require silicate to capture solar energy. It is proposed that the recycling of silicate in upwelling water could be an influential process in the production rate of diatoms (Fu et al. 2001). Similarly, calcite is known to be linked to phytoplankton groups such as coccoliths that have microscopic plating made of limestone (calcite), and occur in cool waters worldwide (NASA, 2002). Analysing these parameters become important in the niche modelling process.

It is important for this study to note that the non-biological environment defines the "fundamental niche"- Areas consisting of all conditions that allow for its survival,

representing a species' potential distribution; a set of environmental conditions that satisfy the reproduction, growth and establishment of a species (Hutchinson 1957). A species' realized niche, is the geographic region the species actually inhabits, which is often a subset of the fundamental niche (Hutchinson 1957).

Other than these environmental influences on the distribution of kelps, the ecology of kelp bed communities is controlled by several other factors, which are not dealt with in this study. These, however, deserve to be mentioned as not only one factor acts at any given time, but rather, a combination of these forces that drive distribution (Rothman et al. 2006). These additional forces impacting the ecology of kelp beds are wave action (Wing et al. 2007, Wernberg and Goldberg 2008), salinity, tides, availability and topography of substrata for attachment (Bekkby et al. 2009), disturbance (Dayton 1998), dispersal, grazing (Dayton 1985) and depth (Bekkby et al. 2009).

Ecklonia maxima

Ecklonia maxima is the only *Ecklonia* species that inhabits the west coast of South Africa. The genus *Ecklonia* is known to only occur where monthly mean temperatures are above 10°C (Bolton and Anderson 1994). At Cape Agulhas, summer monthly mean temperatures were found to be over 21°C (Bolton 1986), which is similar to the temperature at the recently discovered eastern limit of the species, De Hoop (Bolton et al. 2012). Bolton and Levitt (1987) suggest that temperatures greater than 22.5°C are likely to limit the distribution of *E maxima* through their effect on sporophytes, rather than on gametophytes. A seven-day study by Bolton and Anderson (1987) showed that the upper survival temperature of the species is 25°C -<28°C whilst tom Dieck (1993) found that the gametophytes of *E. maxima* had an upper survival temperature of 25°C -26°C. This agrees

with the idea that it is sporophyte rather than gametophyte tolerance of high temps that is important.

Chlorophyll levels are further indicators of productivity in oceans, where high chlorophyll levels are associated with greater phytoplankton biomass, particularly in coastal upwelling regions (Demarcq 2009). Nutrients, associated with upwelling are known to be additional drivers of the species' distribution. Research on the gametophyte phase of *E. maxima* indicates the importance of light in its life history. The saturating irradiance required for growth is less than 20 µmol m^{-2} s^{-1} whilst 15.8°C is the growth and reproductive optimum found under sub optimal light and nutrient conditions during high reproductive periods for *E. maxima* (Bolton 1986).

Ecklonia radiata

The optimum temperature for net photosynthesis of *E. radiata* has been estimated to be approximately 25°C (Staehr & Wernberg 2009). Fairhead et al. (2004) found that lower water temperatures facilitate higher photosynthetic capacity and a negative relationship between recruitment success and water temperature has further been reported (Wernberg et al. 2010). *Ecklonia radiata* is observed to thrive in temperatures of 22.8 to 23.0°C and 23°C is a critical value for sporophytes, where six months beyond this limit may negatively affect sporophyte growth (Hatcher et al. 1987). Populations in northern (warmer) latitudes have a lower resilience to external disturbances compared with southern (cooler) kelp beds, with temperature most likely being the cause (Wernberg et al. 2010).

Other factors such as turbidity and nutrients are critical factor that determine the distribution of *Ecklonia radiata*. Light availability in deeper waters is a concern especially

during periods of climate-induced sediment and nutrient runoff which diminishes water clarity (Vitousek et al. 1997). Novaczek (1984) demonstrated that *E. radiata* spores survived darkness at 10°C, however, they did not survive in the dark at 20°C to 23°C. Nitrogen limitation in *E. radiata* has been found to cause a decrease in photosynthetic rates (Turpin 1991), whilst another common limiting nutrient in kelps is phosphorus (Lapointe et al. 1992).

Ecklonia cava

The coasts of Japan span a wide temperature range, with the eastern coast receiving cold water from the Oyashio Current and the western coast receiving warm waters from the Tsushima Current (Lüning 1990). Warmer temperate localities in Tei, Kochi Pref., southern Japan have temperatures of 15–29°C and cooler temperate localities such as Nabeta, Shizuoka Pref., central Japan have temperatures of 13–25°C (Serisawa et al. 2001). Average SST in Muroto was 21.44°C from 1991–2000 and the yearly average surface seawater temperature in Tanoura was 21.02°C for 1991–2000. Light and temperature are critical factors controlling photosynthesis of kelps, with the optimum temperatures for net photosynthesis for *E. cava* at 400 µmol m^{-2} s^{-1} being 25°C -27°C, whilst a decrease of net photosynthetic rates were observed up to 29°C (Serisawa et al. 2001). Photosynthetic rate increases with the increase of light intensity up to approximately 25µmol m^{-2} s^{-1} and continues until light saturation at approximately 200 µmol m^{-2} s^{-1} which agrees with the light saturation mentioned by Lüning (1990) for middle sublittoral species.

Varying responses to environmental stress such as irradiance or high Photosynthetically Active Radiation (PAR) are displayed by gametophytes and sporophytes, and the potential to resist high light stress is a major factor determining competitive abilities of seaweeds at

the upper limits of their zone (Hanelt 1998). Gametophytes and young sporophytes are sometimes considered as "shade-adapted" algae developing under the adult sporophyte, indicative of their sensitivity to light (Altamirano et al. 2003). The differences among the developmental stages of *E. cava* in sensitivity to high light stress, is attributed to varying protective mechanisms, morphological differences and ecological light adaptations (Altamirano et al. 2004). In the absence of the adult canopy, it is suggested that gametophytes may be the life-history stage that would allow the survival of the population, as well as the genetic variability, in terms of its light adaptation.

Laminaria pallida

A study by Branch (1974) gives evidence that temperature drives the life history of *L. pallida* and the upper survival temperatures are 24.5°C -25°C (tom Dieck 1993). tom Dieck (1993) further observed that gametophytes had an upper survival temperature of 23°C -25°C with differences of - 1.5°C to -1°C at their lower survival temperature. Bartsch et al. (1993) showed that *L. pallida* gametophytes became fertile at 5°C, 11°C and 17°C but not at 21°C, whilst maximum fertility was obtained at 11°C at a photon fluence rate of 9 to 93 g/molm^{-2} s^{-1} and at 17°C at a photon fluence rate of 9 to 41 g/molm^{-2} s^{-1}. This shows that greater irradiance may be more important during exposure periods of lower temperatures. It was shown by Rothman et al. (2017) that along the west coast, turbidity increases northwards, indicating a gradient of decreasing underwater irradiance, which corresponds to the distribution of *L. pallida.* This means that that decreasing irradiance may be a factor limiting the northward distribution of *L. pallida.*

At Robben Island and Oudekraal, summer temperatures below 10°C were likely the result of upwelled water, and winter temperatures were indicative of mixed water (10°C -15°C),

whilst recruitment occurred when temperatures appeared constant at 15°C (Dieckmann et al. 1978). Upwelled water on the South African west coast is associated with cool temperatures between 8°C -10°C and higher nutrient levels, which are also important in the persistence of *L. pallida* in a region (Dieckman et al. 1978).

Laminaria ochroleuca

Laminaria ochroleuca is known to have a northern distributional boundary related to its average winter temperature limit (van den Hoek 1982), which also appears to be its minimum temperature limit (10°C) (Norton, 1977). Similarly, models by Yesson et al. (2015) found the distribution of *L. ochroleuca* to be strongly influenced by winter temperatures, which is further supported by evidence that temperature is in fact a limiting factor for growth and reproduction of the species (Izquierdo et al. 2002). Voerman et al. (2013) presented the optimum temperatures for each life history process, as well as the lethal temperature limits. Gametophyte growth optimum was reported at 15-18°C and lethal limit of 21°C, gametophyte reproduction at a 11/12°C optimum and lethal limit of 18°C, sporophyte growth optimum of 15-20°C and lethal limit of 22-23°C (tom Dieck 1992, Izquierdo et al. 2002). The species has a temperature optimum for spore development between 12°C and 18°C (Izquierdo et al. 2002). Photon fluence rates (irradiance measure) required for development of female gametophytes, maximum fecundity and reproductive success of gametophytes occurred at 40 µmol m^{-2} s^{-1} at temperatures of 15°C, 18°C and 20°C (Izquierdo et al. 2002)**.** Gametophytes of *L. ochroleuca* are infertile at 10°C, whilst sporophytes have an upper lethal limit at 23-24°C (Lüning 1990).

Laminaria ochroleuca was found to respond differently depending on the region where the species is found. For example, heat shock experiments by Pereira et al. (2015) resulted in

French samples to be damaged at 30°C, however, being able to survive this temperature. Portuguese samples, however, were resilient to the same treatment. Water temperature in northern Portugal is usually 15°C in tidal pools and may reach 20°C in warmer summer temperatures, reaching as high as 30°C near the surface (Pereira et al. 2011). In the Mediterranean Sea, *L. ochroleuca* sporophytes have an upper lethal temperature of 22°C – 23°C and are confined to greater depths, thus having to cope with lower photon fluence rates (tom Dieck 1992). In the Strait of Messina (Mediterranean), where the highest temperature of their geographic distribution is found, it is reported that temperature stratification occurs depending on depth. *Laminaria ochroleuca* may have been forced to occur at greater depths because of occasional increase of water temperature above 23°C, or it may be a more shade tolerant species (Pereira et al. 2011). Optimal growth of *L. ochroleuca* sporophytes occurs at temperatures (15–20°C) higher than those for other closely-related species, such as *L.hyperborea*, *L.digitata* (10°C –15°C; tom Dieck 1992), *L.saccharina* (10°C –15°C; Bolton and Lüning 1982) and *L.abyssalis* (15°C –20°C ; tom Dieck and Oliveira 1993). Young sporophytes of Laminariales are known to be adapted to the dim light climate encountered in established kelp communities (Han and Kain 1996) whilst germination in *L. ochroleuca* is independent of photon fluence rate, as observed in other species of *Laminaria* (Lee 1992). John (1969) suggested that the species' range is limited by exposure and light availability. The ability to have high germination rates under all light conditions is advantageous because spores can colonize both shaded and bright regions within a forest.

Niche modelling as a tool

Kelps species are found to occupy regions that satisfy environmental preferences for their growth. It is therefore of concern that a modification of environmental conditions may have

an impact on their distribution, abundance and productivity (Shiel and Foster 2015). One such example is that of Australian habitat-forming

kelp, whose range has contracted due to the increase in extreme climatic events (Smale and Wernberg 2013). Climate change is particularly important in kelp research (Wernberg et al. 2011), therefore being able to map potential global distributions for kelps, based on environmental conditions would give useful information on these systems. Also, in order to understand the impact of any threat, a baseline of species distribution needs to be established (Yesson et al. 2015). This knowledge of species distribution is necessary to undertake further ecological investigations.

One such approach is using Species Distribution Modelling (SDM). During the last two decades, interest in predicting species distributions has grown considerably (Tyberghein et al. 2012). Species distribution modelling has become an important tool in ecology, evolution, biogeography and conservation biology (Graham et al. 2004). Niche-based models essentially represent an approximation of a species' ecological niche using environmental variables that may be relevant to a species' requirements (Phillips et al. 2006). Whilst also explaining ecological suitability, projections are made in geographic space, resulting in an area of predicted presence for a given species. This study utilizes the SDM algorithm, Maxent (Phillips et al. 2006) and the Bio-ORACLE dataset (Ocean Rasters for Analysis of Climate and Environment, 2011) that consists of 23 geophysical, biotic and climate rasters (Tyberghein et al 2011), that will be mentioned in the next section.

The Maxent software package is one of the most popular tools for species distribution and environmental niche modeling, with a great number of published applications since 2006 (Merow et al. 2013). High predictive power has been demonstrated using Maxent and Bio-

ORACLE in successfully modelling the distribution of *Codium fragile,* an invasive seaweed species (Tyberghein et al. 2012). Other uses of Maxent has been used in terrestrial studies to predict suitable habitats for an endangered tree species (Kumar et al. 2009), whilst the specific use of Bio-ORACLE has been used in several studies to model numerous organisms, for example the biogeography of bivalve wood borers (Borges et al. 2014), the distribution of invasive corals (Riul et al. 2013), the spatial extent of the Great Barrier Reef (Bridge et al. 2012) and the spatial segregation of sea birds (Quillfeldt et al. 2013).

The Maxent model is a Maximum Entropy approach to species distribution modelling, which uses known geographic coordinates of where a species has been observed (Phillips et al. 2004). The mechanism of this method will be explained further on in this section. The major outputs of this method are: (1) a habitat suitability map, showing where a species could grow based on its current distribution and the global environmental dataset; and (2) a table of environmental variables and their percentage contributions to the habitat suitability map. At this point it is critical to reflect on the definitions previously provided for a fundamental and realised niche of a species. A fundamental niche is a region in which a species can potentially (but does not necessarily) grow, based on environmental conditions present. The realised niche is where a species is found, that satisfies the environmental requirements of a species. The realised niche can, but is not always, a subset of the fundamental niche. This method therefore aims to provide a view of the potential fundamental niches(s) of the species under investigation.

Bio-ORACLE Environmental Rasters

Tyberghein (2011) created the Bio-ORACLE dataset from existing satellite as well as *in situ* measurements and later (Tyberghein et al. 2012) went on to explain the details of this

process, which is summarised here. The satellite data is comprised of remotely sensed data from various satellite sensors such as Aqua-MODIS, Terra-MODIS-derived cloud fraction data (http://modis-atmos.gsfc.nasa.gov/) at a resolution of 6 arcmin derived monthly and SeaWiFS (http://oceancolor.gsfc.nasa.gov/) at a 5 arcmin (*c*. 9.2km spatial resolution), (Tyberghein et al. 2012). The satellite data were summarized for each month across several years to obtain the final Bio-ORACLE dataset. The satellite data were resampled to a resolution of 5 arcmin, whilst annual ranges of variables such as temperature and cloud cover, were also included in the dataset to represent proxies for seasonality and temporal variations (Tyberghein et al. 2012). *In situ* surface measurements such as salinity, pH, dissolved oxygen, silicate, nitrate and phosphate, were spatially incorporated into the Bio-ORACLE dataset, derived from the World Ocean Database (Boyer et al. 2009). Interpolation was applied using DIVA (Data-Interpolating Variational Analysis), a method developed for gridding *in situ* data (Brasseur and Haus 1991). Global General Bathymetric Chart of the Oceans GEBCO 1-arcmin bathymetry (http://www.gebco.net/) was used in extracting coastlines. The last step of deriving the full Bio-ORACLE dataset was the application of a uniform land mask to all layers to correct discrepancies between environmental data and the coastline (Tyberghein et al. 2012).

The Maxent Method

The models in this study were inferred using Maxent v3.3.3, a maximum entropy machine-learning algorithm, with superior performance in SDMs among presence-only methods (Elith et al. 2011). Maxent is founded on the principle of entropy, an important concept in information theory, and operates by agreeing with everything that is known, whilst carefully avoiding the assumption of anything that is unknown (Jaynes 1990). In this study, Maxent is specifically applied to presence-only SDM, where the pixels of the study area make up the

space on which the Maxent probability distribution is defined. Algorithms used by Maxent guarantee convergence to the optimal (maximum entropy) probability distribution, which allows interpretation of how the environmental variables relates to habitat suitability (Phillips et al. 2004). Maxent uses a set of functions to represent the environmental variables which in this study, are taken from the Bio-ORACLE dataset. By the maximum entropy principle, the probability distribution of maximum entropy is calculated, subject to constraints of the environmental parameters over the distribution. The habitat suitability maps generated in this thesis aim to provide global trends of the important environmental variables.

Aims and Objectives

The aim of this study was to map the distribution of South African kelp species, based on available literature, and to use species distribution modelling to map potential global niches for the South African species. The study aimed to answer four questions:

1. What are the environmental drivers of each species' distribution?

2. Are there regions identified where each species could grow, but don't?

3. Do the three major South African kelp species, *E. maxima, E. radiata* and

   L. pallida , differ in their environmental requirements, given that they are

   on different coasts?

4. Are the potential global distributions different for closely-related *Ecklonia* and

   Laminaria species?

It is intended to explain the results in terms of environmental limits to growth, lethal limits, phylogenetic relationships, and biogeography of each species.

Chapter 2: Methods

Data Collection and Environmental Dataset

Using presence-only occurrence data, Maxent was used to create predictive maps based on current species distributions and their associated global environmental datasets. Occurrence data was obtained for *E. maxima* (n=66)*, E. radiata* (n=358)*, E. cava* (n=69)*, L. pallida* (n=51) and *L. ochroleuca* (n=302) from the available literature as well as the online Global Biodiversity Information Faculty (GBIF) (http://www.gbif.org/species) and Ocean Biogeographic Information System (OBIS)

(http://www.iobis.org/)*.* Occurrence localities were recorded as decimal latitude–longitude pairs denoting known sites where each species has been observed. Reported localities for a species that were not verified or treated as doubtful, were eliminated from the modelling process (Mainali et al. 2015). Knowledge of the habitats and regions greatly facilitated the assessment of sampling bias (Merow et al. 2013). Experts with this knowledge were consulted when deciding on final datasets to be used in the model. The data was viewable via preliminary maps which showed all recorded occurrences in order to fully establish an accurate representation of each species' known distribution, before the modelling process was initiated.

Where the literature named occurrence locations of a species, Lat-Long Maps (http://www.latlong.net/) and Google Maps (http://www.mapcoordinates.net/en) were used to extract exact coordinates, closest to the respective coast or bay. Google Earth (https://www.google.com/earth/) and Earthpoint (http://www.earthpoint.us/) were used to format and adjust coordinates that were too close to land. Carto (https://carto.com/), a

cloud computing platform providing GIS mapping tools, was used to plot maps of species distribution to view density, intensity and distribution limits of points mapped. The final maps of each species' current distribution were created using Carto, and are presented in this study.

Environmental predictors of species distributions can be one of three idealised kinds: direct, resource and indirect (Austin, 1980). Direct predictors have a direct physiological influence on the survival of a species but are not consumed by them (e.g. temperature), resource predictors are consumed (e.g. light, nutrients) and indirect predictors are variables such as cover. And cursory review of marine SDM studies published between 2003 and 2013 shows that 59% of studies choose predictors based on biological reasons, expert opinion or previous studies 31% of studies mention no reason for choosing predictors and the 10% of studies selected predictors based on availability and correlation (Bosch et al. 2017).

The environmental layers used in Maxent were drawn from Bio-ORACLE, which consists of 23 geophysical, biotic and climate rasters (Tyberghein et al. 2011). When compared to other marine datasets Bio-ORACLE fares well in that it has a uniform landmask, uniform file format, equal-area grids and nutrient proxies (Tyberghein et al. 2012). The 23 rasters are: Calcite (cal), maximum (chlomax) chlorophyll, mean chlorophyll (chlomean), minimum chlorophyll (chlomin), chlorophyll range (chlorange), maximum cloud cover (cloudmax), mean cloud cover (cloudmean), minimum cloud cover (cloudmin), maximum Diffuse Attenuation (DAmax), mean DA (DAmean), minimum DA (DAmin), dissolved oxygen (dissox), nitrate, maximum Photosynthetically Available Radiation (PARmax), mean PAR (PARmean), pH, phosphate (phos), salinity, silicate, maximum sea surface temperature (SST) (SSTmax), mean SST (SSTmean), minimum SST (SSTmin), range

SST(sstrange). The abbreviations used in this study will only pertain to DA, PAR and SST, whilst the above-mentioned abbreviations only feature in Jackknife and Table outputs (Appendix A and B). The number of predictors used in a variety of studies ranged from 3 to 26 (Bosch et al. 2017) and in this study all 23 variables were used in the initial modelling process. All 23 variables pertain to the biology of the kelps under study, and the Bio-ORACLE dataset has been used in its entirety in seaweed studies before (Tyberghein et al. 2012; Jueterbock et al. 2013; Verbruggen et al. 2013; Poursanidis D.2015). It should be noted that considerations were taken surrounding multi-collinearity in the variable selection processes.

Model Inputs

Using the environmental layers and occurrence data, the Maxent process assigns a non-negative probability to each point where these probabilities sum to 1. Background data was generated by dividing occurrences into training and test data and which was set at 50. This commands the program to randomly set aside 50% of the sample records for testing and 50% for training. This was randomised. This is in line with Maxent's presence-only algorithm where sub-sampling distribution records is generally the best performing method for reducing bias in sample selection (Fourcade et al. 2014). By default, Maxent uses the number of presences to determine which feature classes to use; more presences allows more features and > 80 presences leads to all feature classes being used. Logistic outputs were provided by Maxent, which gives an estimate between 0 and 1 of probability of presence, assigning a probability of 0.5 to typical presence localities, 0 to areas of no presence, and close to 1 to areas of predicted presence.

Statistical Analysis and Model Performance

Model performance was measured using Area Under a Curve (AUC) of the receiver operating characteristic (ROC) for test data (Phillips et al. 2006). AUC values range from 0 to 1 and models yielding scores for the test data set (AUC_{test}) above 0.5 can be interpreted as better than random predictions. Each species' analysis was replicated five times and the evaluation proceeded through jackknifing. After replications of each species' analysis, the mean relative occurrence or suitability probabilities were used for further analyses (Merow et al. 2013). All AUC values were >0.98, showing excellent performance of all five models. The AUC values for each model are visible on the x-axis of the jackknifes (Appendix A1, Figure 1; Appendix A2, Figure 2; Appendix A3, Figure 3, Appendix A4, Figure 4; Appendix A5, Figure 5).

Variable Selection

Multi-collinearity of variables was avoided by adopting a variable selection method. This was a step-wise procedure, which was performance-based. The jackknife tool in Maxent was used to measure variable importance as well as permutation importance and percentage contribution. The highest percentage contribution values were chosen as the most important variables to the model (Angelieri et al. 2016). There was a large visible discrepancy between high and meaningful values and those displaying percentages close to zero(Appendix A1, Figure 12). Only a subset of variables with higher percentage contribution is presented for the final model. The general observation was that variables with percentage contributions >9% were most important. In addition to this, the jackknife method involved each variable being excluded in turn, with a model being created with the remaining variables. Another model was created using each variable in isolation, revealing the importance of each variable in relation to an optimal model. Important

variables in the AUC jackknife are represented by dark blue bars, whilst light blue bars were used to ensure the model was at an optimum with the utility of a single variable, i.e close to an optimum model, expressed as a red bar (Appendix A1, Figure 1; Appendix A2, Figure 2; Appendix A3, Figure 3, Appendix A4, Figure 4; Appendix A5, Figure 5). Both permutation and percentage values, as well as the jackknife were considered when selecting the most important variables. On the rare occasion where the jackknife showed that the omission of a specific variable would improve the model, yet the same variable obtained low percentage contribution or permutation importance the variable was given the benefit, and included in the model. This was done as AUC values, indicating a better model upon omission of the variable, showed only slight changes, with the model still resulting in an AUC >0.98 upon inclusion of the variable. The variable selection process from the initial model runs yielded 5-8 important environmental variables for each of the species models. Data redundancy and overparameterization were considered and avoided by ensuring that variables represented a variety of environmental parameters. The best set of predictors producing the highest test AUC value (0.98) was used to infer the final models. The final models were run (50% training, 50% test data) with five replicate runs each. The resulting models achieved high classification success, with all species achieving an AUC of $\geq$0.98.

Bio-ORACLE environmental rasters

Temperature

Temperature has been known to be one of the most important drivers of marine species distribution (Wernberg et al. 2011) and is commonly measured as Sea Surface Temperature (SST). Sea surface temperature is an essential and potentially limiting variable for photosynthetic organisms as it provides in their energy needs (Tyberghein et

al. 2012). Varying temperature limits, whether maximum or minimum growth, reproduction or lethal limits, are important for every life history stage of kelps (Breeman 1988). Temperature limits determine the hardiest life history stages as well as revealing sensitive stages of kelp growth, reproduction and ultimately, survival. Temperature limits of a species therefore give rise to their distributions and range limits. This study uses minimum, maximum and mean temperature data from the Bio ORACLE dataset (Tyberghein et al. 2011). This SST satellite data was obtained from Aqua-MODIS, representing temporal values from monthly climatologies, between the years 2002 and 2009. SST range was calculated by subtracting the minimum SST from the maximum SST value (Tyberghein et al. 2012).

This study uses minimum, maximum and mean temperature data from the Bio-ORACLE dataset (Tyberghein et al. 2011). This SST satellite data was obtained from Aqua-MODIS, representing temporal values from monthly climatologies, between the years 2002 and 2009. SST range was calculated by subtracting the minimum SST from the maximum SST value (Tyberghein et al. 2012).

Light

Photosynthetically Available radiation (PAR) represents the light available for photosynthesis. Therefore maximum and mean PAR in SDMs are indicators of upper and average irradiance that may influence species' distribution Monteith (1973) stated that irradiance is approximately 70% under clear skies, 20-50% under broken clouds, whilst deep cloud layers may transmit only 10% of solar radiation. In addition to PAR, maximum, minimum and mean cloud cover is a further indicator of light suitability that may influence species distribution. Cloud cover has the potential to indirectly influence marine organisms.

Clouds can block the transmission of light and harmful UV radiation and affect inter-tidal communities and organisms abounding in the ocean surface layer (Tyberghein et al. 2012).

Diffuse Attenuation (DA) is another variable included in the Bio-ORACLE dataset. DA is an optical property of seawater measuring turbidity of the water column, accounting for the vertical distribution of PAR. DA incorporates depth in its measurement, which is a bathymetric consideration necessary in marine species niche modelling. DA additionally links to the amount of particulate material in the water column. Maximum, minimum and mean DA therefore indicates areas with these conditions that could predict species distribution. Satellite data for DA in the Bio-ORACLE dataset was obtained from Aqua-MODIS, consisting of temporal values from monthly climatologies from 2002-2009. The Bio-ORACLE dataset obtained satellite data for PAR from Sea WiFS, which consist of temporal values from monthly climatologies from 1997-2009. Satellite data for cloud cover in the Bio-ORACLE dataset was obtained from Terra-MODIS, which consist of temporal values from monthly climatologies from 2005-2010.

Chlorophyll and nutrients

Chlorophyll levels are an indication of light-harvesting phytoplankton which require these pigments for photosynthesis. Chlorophyll *a* is a useful proxy for the trophic status of the surface waters (Duan et al. 2007). Chlorophyll is therefore an indicator of productivity and is generally more abundant in cool waters in upwelling regions, with high nutrient content (NASA, 2007). Chlorophyll is a proxy for nutrients, representing the productivity of a system, ie. the amount of nutrients, where low chlorophyll levels suggest low phytoplankton levels and vice versa. Minimum, maximum, mean and range chlorophyll levels therefore indicate nutrient content in a region that may influence species distribution. The Bio-ORACLE

satellite data for chlorophyll are temporal monthly climatologies for the period 2002-2009 taken from Aqua-MODIS.

The use of silicate in modelling is also a measure of productivity of a system that could give insight into marine species distribution. The Bio-ORACLE dataset uses mean silicate data which is a DIVA interpolation of *in situ* measurements taken from WOD (World Ocean Database) 2009. It is proposed that the recycling of silicate in upwelling water could be an influential process in the production rate of diatoms (Fu et al. 2001).

Models also incorporate calcite concentration, a measure of productivity, as well as pH, an indicator of ocean acidity, which can predictor marine species distribution. The Bio-ORACLE dataset uses mean calcite measurements for the period 2002-2009, which are temporal values taken from monthly climatologies on the Aqua-MODIS database. Mean pH values are obtained using DIVA interpolation of *in situ* measurements, from WOD 2009.

The use of phosphate and nitrate are also variables that are part of the Bio-ORACLE dataset which incorporated mean values for each, from a DIVA interpolation of *in situ* measurements taken from WOD 2009. Jackson (1977) reported that the pattern in temperate oceanic waters is for surface waters to be depleted of fixed nitrogen, phosphorus and silicon by phytoplankton growth in summer, and to be enriched during the winter by mixing with a high nutrient subsurface. These environmental predictors are thus important to include in a marine dataset, which could potentially explain marine species distributions.

Salinity gradients and dissolved oxygen levels are also featured in the Bio-ORACLE dataset, which may be likely environmental parameters that could explain marine species distributions. These mean values were manipulated by Tyberghein et al. (2012) using DIVA interpolation of *in situ* measurements taken from WOD 2009.

The output of the SDM process using Maxent and Bio-ORACLE, are resulting habitat suitability maps, highlighting coastlines that correlate with important environmental variables- This is the fundamental niche/potential habitat. In this study, regions identified (highlighted) as potential habitats that were unclear, not distinct enough, or did not form a reasonable stretch of coast, were considered to be inconclusive niche suggestions. The second output is a table of the most important environmental variables along with their percentage contributions and permutation importance to the model. Models are run more than once, to obtain a best model, and permutation importance is calculated on the final Maxent model. The percentage importance is based on the path that Maxent uses to reach the best model. Each step of the Maxent algorithm increases the gain (optimum) of the model by modifying the coefficient for a single feature. A percentage is then given to each variable depending on its importance to the model. Both percentage values were therefore considered when selecting the most important variables. In addition to this, a Jackknife is another statistical output that further evaluates the importance of each variable to the model, which is a tool considered along with % importance and & contribution in variable selection for the optimal model.

Chapter 3: Results

The results show the current distributions of *E. maxima* (Figure 1a)*, E. radiata* (Figure 2a), *E. cava* (Figure 3a)*, L. pallida* (Figure 4a)*,* and *L. ochroleuca* (Figure 5a). Predictive maps for each species, inferred by Maxent are also shown (Figures 1b, 2b, 3b, 4b and 5b). The predictive models for each species predicted the complete realised distributions of each species accurately. The predictive maps present the fundamental niche for each species on a global scale, which denote areas where each species can potentially grow based on suitable environmental conditions in these regions. There are regions in each map where each species could apparently grow, based on the analyses, but do not. Some signals appear stronger than others and speculations regarding faint signals would be inconclusive. Furthermore, faint signals fell reveal low likelihood of occurring. Therefore, whilst faint signals have been noted, only clearly visible signals, with higher likelihoods of occurrence, were the focus.

Five to eight of the most important environmental correlates with distribution emerged from the complete dataset of 23 variables for each species. These are tabulated, along with the final percentage contribution and permutation importance of the most important variables (Tables 1-5). The permutation importance values reveal the most important variables that correlate with the final habitat suitability maps. The highest values of permutation importance indicate the most likely environmental correlates of the distribution of a species.

Ecklonia maxima

Ecklonia maxima is found on the west coast of South Africa, southern Namibia, and St. Paul Island (Figure 1a). Its northern limit is north of Lüderitz and its southern limit lies east of Cape

Agulhas. The predictive model shows very slight signals of potential areas where *E. maxima* could potentially grow (Figure 1b), these being along western and southern Australia, northern Africa and a small segment of the Chilean coastline. The strongest and most apparent signal is its occurrence on the west coast of South Africa. There were eight major environmental variables out of the 23-variable dataset (Appendix A1, Table 1) that the model identified as correlates of distribution of *E. maxima*. These are maximum, mean and minimum SST, maximum cloud cover, maximum PAR, minimum DA, maximum chlorophyll and minimum chlorophyll (Table 1). The model would not be optimal if SST min was omitted from the model, therefore highlighting the importance of this variable to the optimal model (Appendix A1, Table 1). Maximum cloud cover (38.8%), minimum DA (13.6%) and mean SST (11.5%) were all important contributors to the path Maxent took to obtain the optimal model, and maximum cloud cover (38.3%) and maximum SST (55.5%) were the most important variables in obtaining the final model (Figure 1b).

Figure 1a. Map showing the current distribution of *E. maxima* on the South African west coast and St Paul Island*.* Darker colours show high density of samples in a region.

Figure 1b. Habitat suitability map showing predicted areas where *E. maxima* could potentially grow, based on environmental conditions in these regions. Blue indicates low probability values(0-0.3) followed by Green(0.46-0.69),Yellow(0.77) and Orange-Red (0.85-1). Maxent assigns an estimate between 0 and 1 of probability of presence, probability of 0.5 to typical presence localities, 0 to areas of no presence, and close to 1 to areas of predicted presence.

Table 1. Important environmental variables that correlate with *E. maxima* distribution and that contribute to the habitat suitability model. Values bolded are identified as those most important to the model.

Environmental Variable	Percent contribution (%)	Permutation importance (%)
Maximum cloud cover	**49.6**	***38.3**
Minimum DA	**13.6**	0
Mean SST	**11.5**	0
Maximum PAR	8.8	0.3
Maximum chlorophyll	8.3	0
Maximum SST	7	***55.8**
Minimum SST	0.9	5.5
Minimum chlorophyll	0.2	0

*Variables with the greatest importance to the final habitat suitability model

Ecklonia radiata

The current distribution of *E. radiata* shows that the species grows along the south and east coasts of South Africa, Canary Islands, southern Australia, New Zealand and associated islands (Figure 2a). The habitat suitability map (Figure 2b) shows that *E. radiata* could potentially grow in the north Atlantic, northeast Pacific, and southeast Pacific with a faint signal in Madagascar. There were eight major environmental variables out of the dataset of 23 (Appendix A2 Table 2) that the model identified as correlates of distribution of *E. radiata*; maximum, mean and minimum SST, maximum cloud cover, silicate, phosphate, calcite, and minimum chlorophyll (Table 2). The most effective single variable for predicting the distribution, according to the jackknife, is minimum chlorophyll (Appendix A2 Figure 2). Table 2 below shows that calcite (31.5%), maximum cloud cover (23.2%) and silicate (22.7%) were all important contributors to the path Maxent took to obtain the model, whilst phosphate (75%) and maximum cloud cover (41%) were the most important variables to the final model.
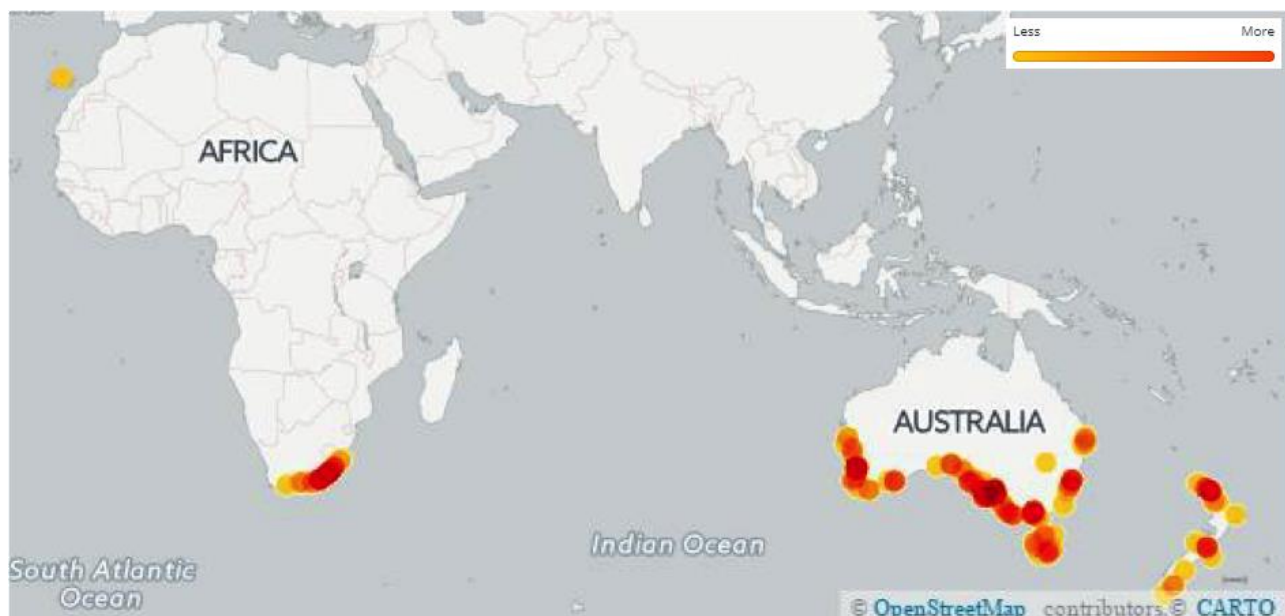

Figure 2a. Map showing the current distribution of *E. radiata* on the south and west coast of South Africa, southern Australia, New Zealand and surrounding islands as well as Canary islands. Darker colours show high intensity of samples in the region.
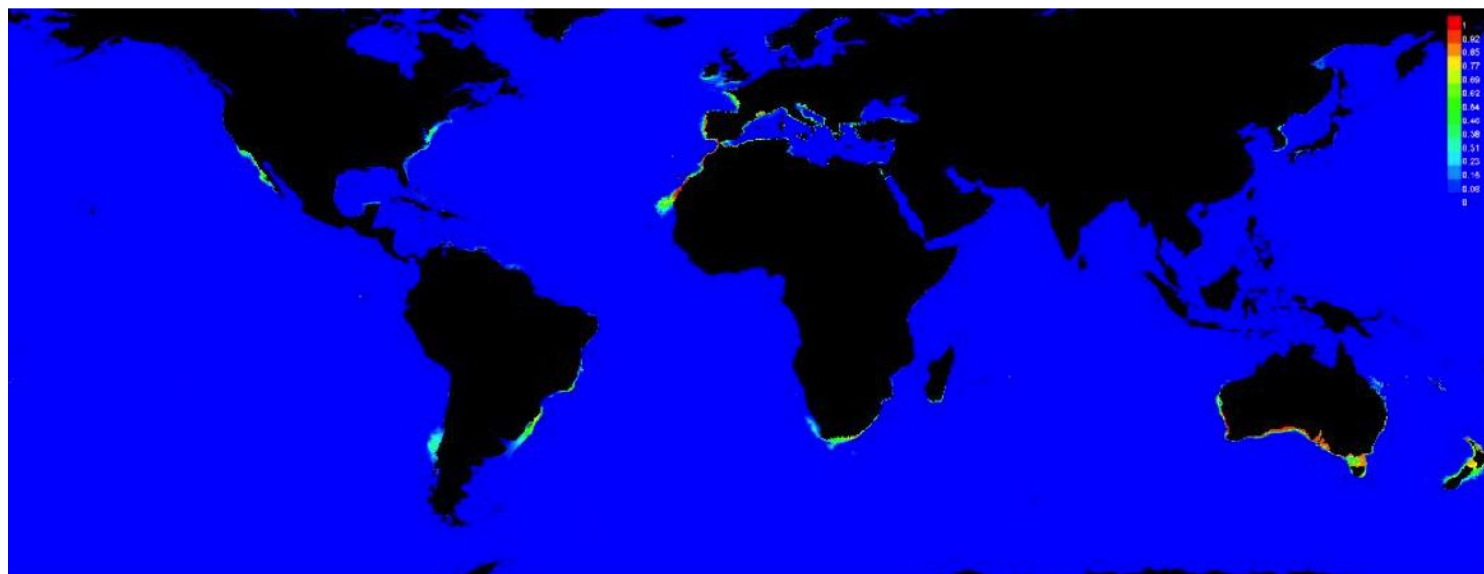
Figure 2b. Habitat suitability map showing predicted areas where *E. radiata* could potentially grow, based on environmental conditions in these regions. Blue indicates low probability values(0-0.3) followed by Green(0.69-0.46),Yellow (0.77) and Orange-Red (0.85-1). Maxent assigns an estimate between 0 and 1 of probability of presence, probability of 0.5 to typical presence localities, 0 to areas of no presence, and close to 1 to areas of predicted presence.

Table 2. Important environmental variables that correlate with *E. radiata* species distribution, and contribute to the habitat suitability model. Values bolded are identified as those most important to the model.

Environmental Variable	Percent contribution (%)	Permutation importance (%)
Calcite	**31.5**	4.8
Maximum Cloud Cover	**23.2**	*14.1
Silicate	**22.7**	0
Maximum SST	7.7	4.7
Phosphate	6.1	**75
Minimum Chlorophyll	5.4	1
Minimum SST	3.6	0.4
Mean SST	0	0

*Variables with the greatest importance to the final habitat suitability model

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Ecklonia cava

Ecklonia cava is distributed on portions of the coasts of Japan and parts of South Korea (Figure 3a). The model found *E. cava* to potentially be able to inhabit coasts of China, the Mediterranean and parts of South America and the Gulf of California to be a potential niche based on its environmental needs (Figure 3b). There are seven major environmental drivers that the model identified out of 23 (Appendix A3 Table 3), which may control the distribution of *E. cava*, these being maximum, minimum, mean and range SST, mean PAR, minimum chlorophyll and silicate (Table 3). The jackknife validated that the most effective single variable for predicting the distribution is SST range (Appendix A3 Figure 3). Table 3 below shows that SST range (37.1%), minimum chlorophyll (21.2%), minimum SST (20.9%) and calcite (15.8%) were most important contributors to the path Maxent took to obtain the model, whilst maximum SST (85.7%) was the most important variable to the final model.
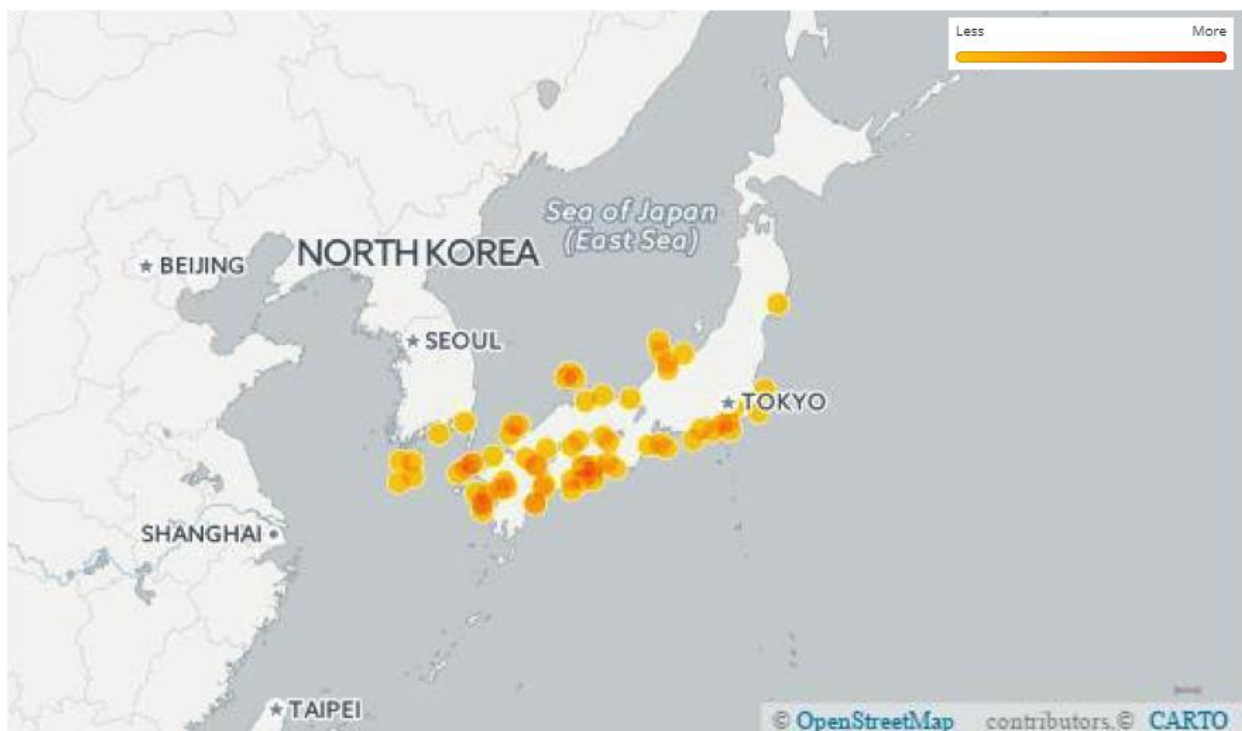

Figure 3a. Map showing the current distribution of *E. cava* on the coast of Japan and South Korea. Darker colours show high intensity of samples in the region.
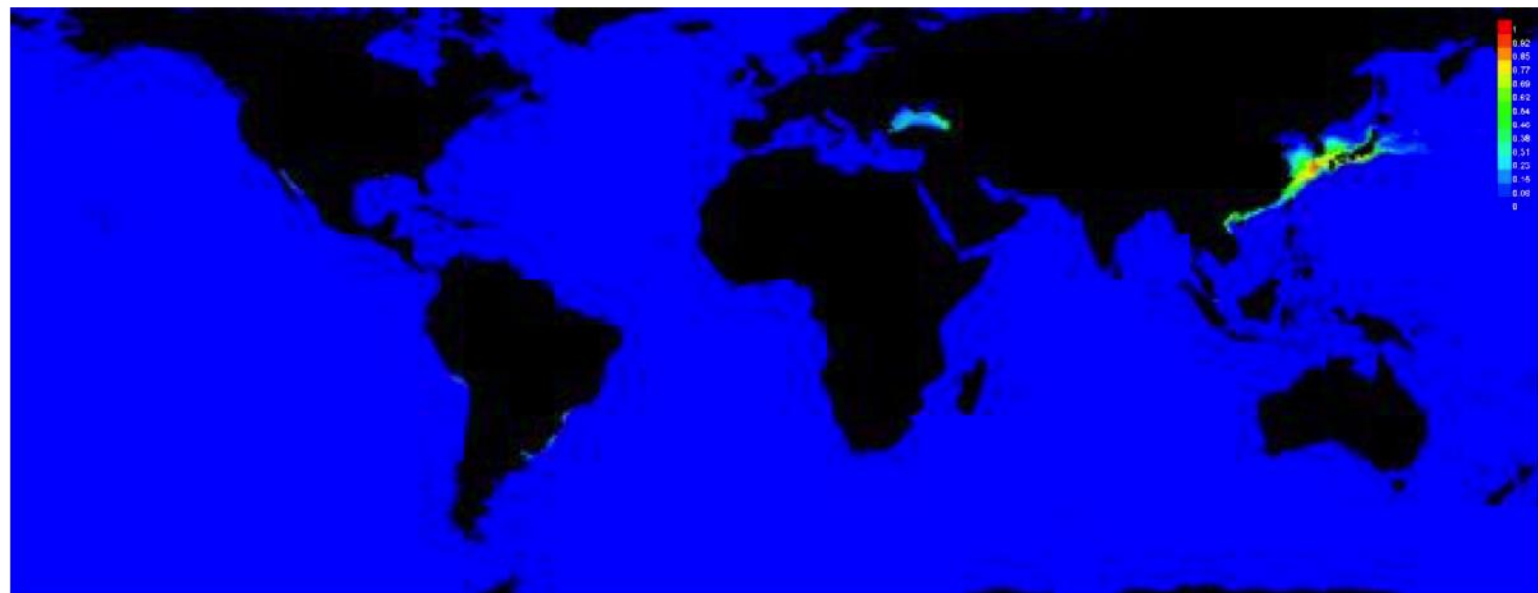
Figure 3b. Habitat suitability map showing predicted areas where *E. cava* could potentially grow, based on environmental conditions in these regions. Warmer colours indicate that the species is more likely to be able to occur in a region. Blue indicates low probability values(0-0.3) followed by Green(0.69-0.46),Yellow (0.77) and Orange-Red (0.85-1). Maxent assigns an estimate between 0 and 1 of probability of presence, probability of 0.5 to typical presence localities, 0 to areas of no presence, and close to 1 to areas of predicted presence.

Table 3. Important environmental variables that correlate with *E. cava* species distribution, and contribute to the habitat suitability model. Values bolded are identified as those most important to the model.

Environmental Variable	Percent contribution (%)	Permutation importance (%)
Range SST	**37.1**	0.3
Minimum Chlorophyll	**21.2**	6.8
Minimum SST	**20.9**	0
Silicate	**15.8**	0.6
Mean SST	3.2	2.7
Maximum SST	1.1	***85.7**
Mean PAR	0.7	3.8

*Variables with the greatest importance to the final habitat suitability model

Laminaria pallida

Laminaria pallida grows along the west coast of South Africa and Namibia (Figure 4a). The niche model shows that it could grow on the west coast of South America, southeast South America, northwest Africa and western Australia based on environmental conditions in that region (Figure 4b). The major environmental drivers that the model identified, which may

control the distribution of *L. pallida* are maximum, minimum and mean SST, maximum PAR and maximum DA (Table 4). The jackknife shows that the environmental variable with highest gain when used in isolation is maximum DA, which appears to have the most useful information by itself whilst the environmental variable that decreases the model optimum the most when it is omitted, is maximum DA, which appears to have the most information that isn't present in the other variables (Appendix A4, Figure 4). Table 4 shows that maximum PAR (60.1%) and maximum DA (31.7%) were important contributors to the path Maxent took to obtain the model, whilst maximum PAR (51.2%), minimum SST (20.2%) and mean SST (25.6%) were the most important variables to the final model.

Figure 4a. Map showing the current distribution of *L. pallida* on the west coast of Southern Africa and Amsterdam Island. Darker colours show high intensity of samples in the region.
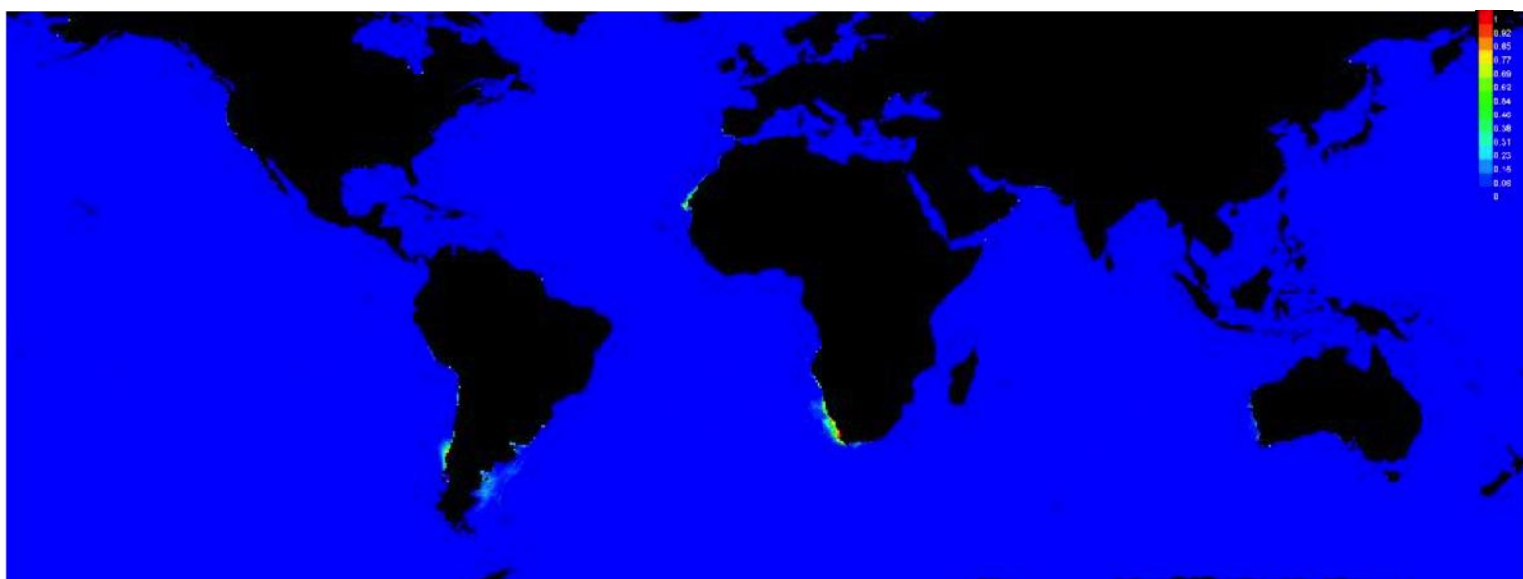
Figure 4b. Habitat suitability map showing predicted areas where *L. pallida* could potentially grow, based on environmental conditions in these regions. Warmer colours indicate that the species is more likely to be able to occur in a region. Blue indicates low probability values(0-0.3) followed by Green(0.69-0.46),Yellow (0.77) and Orange-Red (0.85-1). Maxent assigns an estimate between 0 and 1 of probability of presence, probability of 0.5 to typical presence localities, 0 to areas of no presence, and close to 1 to areas of predicted presence.

Table 4. Important environmental variables that correlate with *L. pallida* species distribution, and contribute to the habitat suitability model. Values bolded are identified as those most important to the model

Environmental Variable	Percent contribution (%)	Permutation importance (%)
Maximum PAR	**60.1**	***51.2**
Maximum DA	**31.7**	3
Maximum SST	4.8	0
Minimum SST	2.2	***20.2**
Mean SST	1.2	***25.6**

*Variables with the greatest importance to the final habitat suitability model

Laminaria ochroleuca

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Laminara ochroleuca is found in the Northeastern Atlantic region, on the coast of Britain, France, Spain, Portugal and Morocco (Figure 5a). The niche model showed the realised niche well, and further predicted that the species has a high likelihood of being able to grow on the west coast of Ireland, with faint signals of potential niches in southern Australia, the

coastline of New Zealand, North America, South America and the Mediterranean (Figure 5b).

Seven major environmental drivers were identified as important to the distribution, out of

23 variables (Appendix A5 Table 5). These are maximum, minimum and mean SST, calcite,

silicate, minimum chlorophyll and phosphate (Table 5). The jackknife showed that minimum

chlorophyll on its own was the variable that provided the most unique information to the

model (Appendix A5 Figure 5). Table 5 below shows that calcite (54.6%), maximum

chlorophyll (11.8%) and minimum SST (11.6%) were important contributors to the path

Maxent took to obtain the model, whilst phosphate (59.3%) and minimum chlorophyll

(27.6%) were the most important variables to the final model.

Figure 5a. Map showing the current distribution of *L. ochroleuca* on the coasts of Britain, Spain, France, Portugal, Morocco and North Atlantic Islands. Darker colours show high intensity of samples in the region

Figure 5b. Habitat suitability map showing predicted areas where *L. ochroleuca* could potentially grow, based on environmental conditions in these regions. Warmer colours indicate that the species is more likely to be able to occur in a region. Blue indicates low probability values(0-0.3) followed by Green(0.69-0.46),Yellow (0.77) and Orange-Red (0.85-1). Maxent assigns an estimate between 0 and 1 of probability of presence, probability of 0.5 to typical presence localities, 0 to areas of no presence, and close to 1 to areas of predicted presence.

Table 5. Important environmental variables that correlate with *L. ochroleuca* species distribution, and contribute to the habitat suitability model. Values bolded are identified as those most important to the model

Environmental Variable	Percent contribution (%)	Permutation importance (%)
Calcite	**54.6**	0.1
Minimum chlorophyll	**11.8**	*27.6
Minimum SST	**11.4**	5.8
Mean SST	8.5	2.6
Silicate	5.7	0.7
Maximum SST	5.3	3.8
Phosphate	2.7	*59.3

*Variables with the greatest importance to the final habitat suitability model

Chapter 4: Discussion

Model Interpretation

This section clarifies comparative differences in the importance of environmental variables in the permutation models for each species, which explains their relative importance to the habitat suitability maps. The three South African species (*E. maxima, E. radiata* and *L. pallida*) differ in their most important environmental variables correlating with distribution, even though *E. maxima* and *L. pallida* have similar distributions. There are two ways of knowing whether a variable is important to the final habitat suitability map/model: (1) High permutation value and (2) High AUC value upon inclusion of variable in model OR Low AUC value upon omitting variable from model. The relative importance of variables can be seen directly from comparing the permutation values. Since the AUC jackknife and permutation tables were considered equally in the variable selection process, it cannot be said with certainty which analysis provides the best answer. Both considerations (1) and (2) were employed in assessing variable importance. Relative importance of values can be further gauged from % contribution values that give insight into the *process* to obtaining the final model.

For *E. maxima*, maximum SST had the highest permutation value followed by maximum cloud cover. In addition to this, the AUC value for the final model would have been reduced without the inclusion of minimum SST in the final model. The *E. radiata* model explains that phosphate had the highest permutation value followed by maximum cloud cover. *E. cava* models showed that the maximum SST permutation value was the greatest whilst SST range contributed the most out of all the variables, to the ideal model. Other variables were mostly important to the *process* of arriving at the final model for *E. cava*. The model for *L. pallida* can be interpreted as maximum PAR having the highest permutation value, followed by mean SST

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and lastly minimum SST. In support of this, the AUC value for the final *L. pallida* model would have been reduced without the inclusion of minimum SST, mean SST and maximum DA in the final model. The model performance for *L. ochroleuca* revealed that phosphate permutation value was the greatest followed by minimum chlorophyll.

Ecklonia maxima

Ecklonia maxima has a unique distribution in that it is only found on the west coast of South Africa*. S*light signals of potential niches are visible; Chilean coast, southern and western Australia. Maximum SST emerged as the strongest correlate of distribution whilst minimum SST contributed greatly to the optimum model. The identified regions have similar minimum and maximum SST to the west coast of South Africa (Appendix B, Figure 7 and 8) whilst the west coast of South America are upwelling regions, potentially serving as ideal niches in this regard. However, these are not the only environmental conditions that may drive the species distribution. Maximum cloud cover, an indicator of irradiance, is also an important correlate of distribution which suggests that the occurrence of *E. maxima* may be largely influenced by light. Minimum DA was also important in the process of arriving at the final model, which is an indicator of water turbidity, light and particulate matter. Consequently, light appears to be a consistently strong correlate of species distribution. This is not unfounded as Bolton (1986) reported a saturating irradiance for *E. maxima* gametophyte growth, as well as temperature optimums for growth and reproduction under suboptimal light.

The monthly maximum SST (Appendix B, Figure 8) of the Southern African west coast of its distribution is ~16°C at its northern limit, to ~19°C at its southern limit, (Appendix B, Figure 7), whilst the monthly minimum SST stands at ~11°C at the northern limit and ~15°C at its

southern limit. This satellite data shows that the temperature of the region ranges between 11 and 19°C which is consistent with mean temperature values recorded for the southwestern coast of South Africa; warmest months 13-19°C, and coldest months 11-14°C Bolton (1896). Bolton and Anderson (1994) reported that the genus *Ecklonia* is known to only occur where monthly mean temperatures are above 10°C, which is apparent according to the distributional record of *E. maxima* and the satellite temperature data recorded for the region. In an early study by Papenfuss (1942) regions of False Bay where *E. maxima* was absent, was suggested to be caused by high temperatures that prevail during the summer months. This indicates that maximum SST may well be limiting to the species' distribution. Temperatures greater than 22.5°C were suggested to limit the distribution of *E maxima* through their effect on gamentangia (Bolton and Levitt 1987), whilst an upper survival limit of 25°C is recorded for the species (Lüning 1990). Sufficient research on temperature effects on the growth and reproduction of large sporophytes of *E. maxima,* is yet to be done.

Temperature (minimum and maximum SST) and light (cloud cover) are likely drivers of *E. maxima* distribution, according to this study as well as previous research done on the species (Bolton 1986, Bolton and Levitt 1987, Lüning 1990, Bolton and Anderson 1994). It would be premature to assume that *E. maxima* could grow in the highlighted regions as these signals are faint as well as have an occurrence probability of <0.5. It is therefore very likely that the environmental requirements of *E. maxima* are rare in other regions of the world. The model therefore shows the realised niche of the species as the only likely potential niche, which indicates that the distribution of *E. maxima* is unique, and unlikely to be able to grow anywhere else in the world.

Ecklonia radiata

Ecklonia radiata is distributed along the south coast of South Africa and southern Australia, as well as New Zealand, Tasmania and other associated islands. *Ecklonia radiata* has also been reported in the north Atlantic (Canary and Cape Verde Islands) (Bolton and Anderson 1994) and sighted in Senegal, Mauritania and in Oman. *Ecklonia radiata* can potentially grow further in the North Atlantic, northeast Pacific, southeast Pacific and Madagascar.

The most important correlate of distribution of *E. radiata* is phosphate. Phosphate is known to be a common limiting nutrient in kelps (Lapointe et al. 1992). Minimum chlorophyll (a proxy for dissolved nutrients) was also an important variable contributing to the model whilst silicate and calcite were important variables to the process of obtaining the final model. Branch (1974), who considered factors playing a limiting role in the distribution of the Laminariales of South Africa, further suggested that nutrient availability is of prime importance. The southern coast of Australia *E. radiata* is found where the nutrient concentrations are extremely high favouring macroalgal growth (Lüning 1990). In regions where *E. radiata* could potentially grow but does not, nutrients could well be limiting to its distribution.

Cloud cover, an indicator of light is also a correlate of distribution of *E. radiata.* Cloud cover is an indirect predictor, explaining light penetration and irradiance. This is ultimately linked to photosynthesis and growth hence being critical to establishment of *E. radiata* (Wernberg et al. 2010).

Mean, maximum, minimum SST were important variables identified in the initial model which consequently played a role in the final model, albeit small. Evidence for the effect of temperature on *E. radiata* is extensive, providing likely reasons why aspects of temperature may limit distribution. The species grows in a variety of temperature conditions 17-19°C (southern Australia), 14-19°C (South Africa), 6-14°C (southern New Zealand) (Lüning 1990). *Ecklonia radiata* populations from lower (warmer) latitudes were found to have 50% lower photosynthetic rates and 90% lower respiration rates at their optimum temperature than populations from higher (cooler) latitudes (Staehr and Wernberg 2009) which indicates that *E. radiata* is an adaptive species that survives a range of temperatures.

It has been reported that negative correlations between kelp productivity and temperature were found during summer for *E. radiata* on the coast of Perth, Australia (Kirkman 1984). A negative relationship between recruitment success and water temperature has also been demonstrated for certain life history stages (Wernberg et al. 2010). Fairhead et al. (2004) further highlighted that increased warming could negatively impact the density and distribution of *E. radiata* via reduced growth (Hatcher et al. 1987), success of microscopic stages (Mabin et al. 2013), reproductive output (Mohring et al. 2013) and ultimately survival (Wernberg et al. 2013). Kirkman (1984) proposes that low tolerance of sporophytes to high temperatures may limit the distribution of the species (Hatcher et al. 1987). The potential niches may not be occupied due to temperatures at which certain life history stages of the species may not be able to withstand in reaching these areas (Staehr and Wernberg 2009).

Furthermore, some of the potential niches are in upwelling regions, and where this is common, El Niño events could halt upwelling, and therefore nutrient circulation, thereby threatening populations, making it more difficult for new individuals to recruit in this area of

high risk (Tegner and Dayton 1991). Lastly, currents may obstruct dispersal, which is exacerbated by the fact that most macroalgae have limited long-range dispersal properties (van den Hoek, 1987) which could have implications for colonising other suitable regions. Warming, limited light and nutrients, and species dispersal barriers seem to be limitations to potential distribution of *E. radiata* (Wernberg et al. 2010)*.

Ecklonia cava

Ecklonia cava grows on the coast of Japan and South Korea and is predicted to be able to grow on the coast of China, the Mediterranean, South America and the Gulf of California. The model identified SST range and maximum SST as strong correlates of distribution. It is fitting that the model predicted China as a potential niche as the synonymous species (Rothman et al. 2015) E. kurome is known to exist along the coasts of the Chinese provinces region Zhejiang and Fujian (Lüning 1990, Bolton 2010, Guiry and Guiry 2014). It is well known that Japan has a wide temperature range which does not prevent the growth of kelp species. The optimum temperatures for net photosynthesis for *E. cava* at 400 µmol m^{-2} s^{-1} being 25°C -27°C, whilst a decrease of net photosynthetic rates is observed up to 29°C (Lüning 1981). Sakanishi et al. (1988) found that *E. cava* bladelets formed under higher summer temperatures were equipped to endure higher temperatures.

Ecklonia cava was found to decrease when water temperature exceeded 20°C under light conditions of under 5 micromoles m^{-2} s^{-1}, whilst the dark respiration rate increased with temperature rise (Serisawa et al. 2004). Light is an additional factor which determines the success of various life history stages of the species (Altamirano et al. 2004). It is anticipated that the net production of *E. cava* decreases with temperature rise, making maximum temperature limits important to the species. Temperatures as low as 10°C are recorded in

Japan (Appendix B, Figure 8), further highlighting the large range that the species spans, which distinctly characterises the coastline of Japan.

The current distribution of Japanese *Ecklonia* is unique which could be owing to the distinct wide temperature range of the region, which is rare or absent in other parts of the world. In areas such as the North Sea and Labrador Sea in the North Atlantic, which may exhibit suitable temperature extremes, the model clearly shows that it is unlikely that *E. cava* could grow here. The similar reasons are likely for difficulty in establishment in South America, the Mediterranean and the Gulf of California.

Laminaria pallida

Laminaria pallida is endemic to the west coast of South Africa and Namibia and is predicted to potentially grow on the coasts of North Africa, western Australia and South America. Similar to the distribution of *E. maxima,* both the realized and fundamental niches are upwelling regions, presumably suitable in terms of cool temperature and associated nutrients in the region, but may be limited in terms of other factors. Light is one such factor that may be limiting to its distribution, especially as *L. pallida* grows in deeper waters in the south (Rothman et al. 2017). The model predicted that maximum PAR was the greatest correlate of distribution, along with minimum and mean temperature. This is not surprising as It has been stated that the two most important factors influencing (the early developmental stages) kelps are temperature and irradiance levels (Lüning 1980).

The temperature regime for the South African west coast has been well explained previously, having a unique environment that supports cool temperate species. The South African west coast exhibits a mean of 15-20°C which is similar to that of the fundamental niches identified

in the model and could consequently be a likely limit the occurrence of *L. pallida* elsewhere in the world. Temperature is a crucial requirement for multiple life history stages of *L. pallida* (Bartsch et al. 1993) such as an upper survival limit of 25°C whilst limits for the formation of gametangia is below 18°C (Branch 1974). Minimum temperature limits, which was important to the model can possibly restrict stages of development of *L. pallida* which ultimately affects the species distribution.

PAR is a realistic correlate of distribution of this species, as well as DA max indicating irradiance and turbidity respectively. Turbidity was found to be a driver of *L. pallida* distribution, at its northerly limit and it is expected to be able to outcompete *E. maxima* northward, as it overlaps its range (Rothman et al. 2017)*. Laminaria pallida* is thought be adapted to low light, given that a decrease in underwater light corresponds with an increase of the species in the inshore environment (Rothman et al. 2017).

Laminaria ochroleuca

Laminaria ochroleuca is present on the coast of Britain, Spain, Portugal, France and North Africa and is predicted to be able to potentially inhabit southern Australia and New Zealand, North and South America and the Mediterranean. Although the conditions may be suitable in these regions the species probably does not grow here as dispersal barriers, oceanographic currents or geographical barriers may have prevented *L. ochroleuca* from reaching this region. The model identified phosphate and minimum chlorophyll as important correlates of distribution which indicates that nutrients are important factors which could limit where the species can grow.

It is reported that several factors act on the distribution of *L. ochroleuca* and it is generalised that the lower limit is physiologically constrained by light, whilst the upper limit by temperature, humidity, emersion, exposure, grazing and competition (Lüning 1990). The latitudinal distribution of kelps is said to be controlled by light temperature at higher latitudes, and nutrients, temperature and competition at lower latitudes (Lüning 1990). Although nutrients emerged as most important for this model, it must be noted that the model identified temperature (mean, minimum and maximum), and nutrients (calcite, silicate and phosphate) as important correlates of *L. ochroleuca* distribution.

The lack of light-related variables in the model is supported by the fact that *L. ochroleuca* is not heavily dependent on light. Young sporophytes of Laminariales are adapted to the dim light (Han and Kain 1996) and spores have an ability to have high germination rates under all light conditions.

Laminaria ochroleuca has a lower temperature limit of 10°C at its winter isotherm (van den Hoek, 1982) and coincides with the mean SST isotherm of 20°C at its southern limit of Morocco and Western Sahara (Lüning 1990). The species' upper lethal limit is around 22-23°C (tom Dieck 1992) with a temperature optimum for spore development between 12°C and 18°C (Izquierdo et al. 2002). Cool temperatures north of Britain's current distribution of

Laminaria ochroleuca is a major limiting factor in establishment further north. The northeast Atlantic is also known to be warming causing expected decreases in macrophyte biomass (Krumhansl and Scheibling 2012). Tuya et al. (2012) also expressed their concerns on kelp retreat in a northerly direction along the coast of Portugal, indicating a contraction in the range of cold temperate kelp. Poleward shift in kelp distributions were also predicted by

Harley et al. (2012), whilst in the UK, both increased temperature and wave exposure have limited macroalgal distribution (Hawkins et al. 2009).

There are a few likely reasons why *Laminaria ochorloeuca* is said to be able to grow in the Mediterranean but does not. It was found that populations of several large brown seaweed species in this region have fluctuated which is primarily associated with changing predation (Trowbridge et al. 2013). SDMs were also previously performed on *L. ochroleuca* which also showed that it could grow in southwest Ireland. The reason it was thought to not have colonised this area already is dispersal barriers or salinity barriers in the Bristol channel (Brodie, personal obs).

Environmental correlates of distributions, and current and predicted niches of closely-related *Ecklonia* species

As a general comment on species distribution, it is important to note that many environmental gradients co-vary at broad spatial scales, which makes it challenging to attribute causality to one factor (Kain 1989). Nevertheless, many species of macroalgae have distribution ranges spanning temperature gradients of several degrees Celsius, and can grow and reproduce over a wide temperature range (Bolton and Lüning 1982). The broad tolerance of kelp suggests that they may have an ability to adjust and optimize photosynthesis and respiration to the prevailing temperature conditions. Other factors, whose effects are not analysed in this study, may also impact kelp distribution on global, regional and local scales. The likely limiting factors of distribution and the colonisation of fundamental niches include lack of spore transport; substrate (lack of rocky habitats), wave action, currents and predators (Field and Griffiths 1991).

It is hypothesized that *Ecklonia* may have spread from the Northwest Pacific to Australia and lastly to South Africa (Bolton 2010). South African *Ecklonia* could have therefore come either from Australia (via the West Wind Drift) or from Japan (perhaps via Oman). All three closely-related *Ecklonia* species display distinctly different distributions. *Ecklonia maxima*, is found on the west coast of Southern Africa. The species is endemic to this region and is not found on any other continent in the world, nor substantially predicted to be able to grow anywhere else in the world. This indicates that the upwelling west coast of South Africa is a unique region satisfying all environmental, physical and biological conditions for the growth of *E. maxima*. *E. radiata* occupies the southern and western warm temperate coast of South Africa as well as southern Australia and New Zealand and is distinct from that of *E. maxima* (besides the recently discovered limit in De Hoop). The predicted areas of potential growth according to the model are also distinctly different from those predicted for the other *Ecklonia* species. The distribution of *E. cava* is confined to the Pacific regions of Japan and South Korea, which is a completely separate area from that of the other two *Ecklonia* species, as well as its predicted distribution on the coast of China. Being the only Northern Hemisphere *Ecklonia* species under study, Japan has unique temperature ranges well suited to the various life history stages and survival of *E. cava*. According to Lüning (1990) Japan has records of 10°C winters and tropical summer means of 25–28°C. Some of the highest temperature tolerances of kelp gametophytes of up to 29°C have been recorded only for Japanese kelps (Bolton 2010). These wide temperature ranges may require adaptations to the wide temperature ranges, which may not be suitable for non-Japanese kelp species, hence the unique distribution of *E. cava* on the Japanese and Korean coastline.

All three *Ecklonia* species models identified two or more of maximum, minimum, mean and range temperature, as correlates of distribution. The models further identified the strongest

correlates specific to each distribution, which differed from each other: *E. maxima* - maximum SST, minimum SST and cloud cover; *E. radiata* - phosphate, minimum chlorophyll and cloud cover; *E. cava* - maximum SST and SST range. Whilst these may have highlighted likely limits to the species distributions, it was found that temperature, light and nutrients are general requirements for kelp life histories that certainly do not act separately, all imposing some effect on the species and hence distribution.

Environmental correlates of distributions, and current and predicted niches of closely-related *Laminaria* species

Laminaria pallida and *L. ochroleuca* have two completely different distributions, with the former on the west coast of South Africa, and the latter in the Northeast Atlantic. The distribution of *L. ochroleuca* distribution is characterised further by nutrients (phosphate and minimum chlorophyll) whilst the distribution of *L. pallida* is characterised predominantly by irradiance (PAR) and minimum and mean temperature. Temperature variables were correlates of both distributions, with general temperature ranges for both *Laminaria* species being similar, possibly owing to their co-evolution and associated adaptations.

The genus *Laminaria* is hypothesized to have originated in the North Pacific (Lüning 1990). The long-distance dispersal of *Laminaria v*egetative gametophytes, giving rise to the Brazilian and South African *Laminaria* species, is likely due to the high temperature tolerance (25 to 26°C) of the species (Peters and Breeman 1992). Lüning (1990) and tom Dieck (1990) proposed that Southern Hemisphere populations are possibly derived from a dispersal event involving a North Atlantic ancestor of *L. ochroleuca,* where the Brazilian and Southern African

Laminaria species arose by dispersal from a crossing through the tropics, which seems plausible, considering the occurrence of *L. pallida* on the mid-South Atlantic islands.

According to Brierley et al. (2007), reductions in the North Atlantic Current could have major implications for Northern Europe as the cooling that this might bring would deliver less heat northwards (Brierley et al. 2007). This runs counter to the 'global warming' paradigm, however, emphasizes the importance of regional considerations in niche modelling verses global generalizations. As global sea temperatures increase, *L. ochroleuca* is predicted to move northward, such as the case for kelps in Portugal, UK, along with a general trend of poleward shifts of kelp species (Hawkins et al. 2009, Harley et al. 2012, Tuya et al. 2012).

South African species distribution and environmental requirements

Ecklonia maxima and *L. pallida* overlap in much of their distribution, whilst *E. radiata* is found on a different part of the coast. All the South African kelp species can withstand temperatures as low as 10°C at some point of their life history. Maximum, mean and minimum temperature emerged from our models as correlates of all three species distributions. Both west coast species distributions correlated with PAR, as well as chlorophyll (a proxy for nutrients). *Ecklonia radiata* models showed a correlation with nutrients, (phosphate, silicate and calcite), which did not emerge as important drivers for any of the other South African species. Silicate was a rare correlate of distribution of the two species occurring outside of South Africa. *L. pallida* and *E. maxima* distributions were correlated with light and temperature. This makes sense as *L. pallida* occurs in deeper waters in parts of its range, hence turbidity playing an important factor in light regulation. The three South African species' distributions are ultimately all correlated with a combination of temperature, light, and nutrients.

Limitations of this study

Limitations of this study can be attributed to shortcomings in the environmental dataset used, as described by Tyberghein (2011). One such challenge is that the spatio-temporal variability characterizing the oceans can hinder SDM along with the restricted availability of marine data. These biases (and resulting uncertainties) are most pronounced at high latitudes. For example, chlorophyll and PAR, which is measured at relatively short wavelengths, cannot be accurately measured during the winter season at high latitudes due to high solar zenith angles (Gregg and Casey, 2007). The difference between *in situ* vs satellite data has also been a topic of investigation that is receiving more attention, especially in the context of South African coastal SST records (Smit et al. 2013). Some studies show that satellite data may not provide the resolution required for coastal studies, or may not be able to consider factors such as depth. Furthermore, Smit et al. (2013) suggests that in order to arrive at a causal understanding of determinants of biogeographical patterns, temperature is best measured directly.

Of course, with any SDM, there is apprehension of correlations without causation, and concerns of whether certain environmental factors are causational or merely correlated, however, studies (e.g. Tyberghein et al. 2012; Quillfeldt et al. 2013; Riul et al. 2013; Borges et al. 2014) allow us to be confident about the use of Bio-ORACLE and Maxent.

Future Research

This study focused on the current and potential distributions of three ecologically and economically important South African kelp species and their close relatives, as well as environmental correlates of their distributions, using satellite and *in situ* data. The method

used in this study and by others (e.g. Verbruggen et al. 2009; Pauly and De Clerck 2010; Tyberghein et al. 2012) can be used to conduct similar research on the same or other species, using future projections of climatic scenarios or *in situ* environmental data comparisons for more local scale modelling.

I would further like to propose and be part of future research involving an experimental analysis of the temperature tolerances of *L. pallida*, as well as other South African kelp species. A study conducted by Pereira et al. (2015) demonstrated temperature tolerances of French and Portuguese isolates of *L. ochroleuca*, which would be relevant to its sister species *L. pallida.* Such a study has not been conducted on South African *Laminaria* species and would be interesting since the results of such a laboratory experiment would be comparable to that of *L. ochroleuca*, providing novel insight into actual temperature thresholds. This would also be measuring the effect of short warm events in a laboratory setting, and investigating the impacts of high temperatures on the species. Furthermore, for the kelps under study, data is only available on microscopic gametophytes, which are easy to grow (apart from data available for small sporophytes of *Ecklonia* species). There is scope for future studies on larger sporophytes and their growth and reproductive limits relating to environmental factors.

Conclusions

This study has addressed all intended aims and objectives and provided insight into South African kelp species, their distributions, potential distributions and possible environmental drivers. It has also provided a global context of some kelp species by investigating Japanese and European kelp species distributions, that are close relatives of ecologically and economically important South African kelp species. The models identified temperature (maximum, minimum, mean, range), light (DA, PAR, cloud cover) and nutrients (Chlorophyll, phosphate, silicate, calcite) as correlates of species distribution. The study has re-affirmed that *E. maxima, E. radiata* and *E. cava* have unique distributions and potential distributions, and have the same subset of potential drivers that are important to the species' distributions.

Specific correlates of distribution between each species differed. Differing distributions for closely-related *L. pallida* and *L. ochroleuca* were re-affirmed. Environmental correlates of distribution also differed between *Laminaria* species. Temperature proved to be a central influence of all species distributions regardless of whether the models identified it as the strongest correlates of distributions. The two *Laminaria* species exhibited similar temperature tolerances, whilst the three *Ecklonia* species were found to thrive in different temperature regimes. *E. maxima, E. radiata* and *L. pallida* showed distinct patterns of distribution along the South African coast, which correlated with environmental conditions as well as phylogenetic similarity.

This study acknowledges that abiotic conditions apply across wide geographic scales, among regional sites, down depth gradients and over time, which is why one cannot arrive at a single conclusion as to what controls kelp distribution. A variety of factors play a role in

kelp distribution besides the physiological limits investigated in this study. The disparities between regional and global drivers are also important considerations in analysing species distributions.

The results in this body of research presented interesting and useful information on the biogeography of South African kelp and explored global patterns and drivers of closely-related kelps. Since kelp is a keystone species which may underpin other species' range shifts, the results of this study could improve understanding of processes that are likely drivers of changing species distribution. The results of this study could also have applications in aquaculture in terms of knowing where each species grows and can potentially grow, for commercial use. Kelp conservation planning is another area where the data in this study can be used, especially when analysing drivers of niche shifts due to changing climates. Anthropogenic climate change is driving redistributions of marine species at a global scale, and having insight into potential scenarios of reshuffling of communities and entire ecosystems could assist in kelp conservation planning. This study could further assist in providing useful distribution information for marine protected area management and spatial planning, highlighting areas of potential kelp establishment in South Africa and even globally, which may be regions of conservation concern. This study ultimately provides an account of the usage of SDM as a tool in understanding kelp interactions with the environment, providing global insights to environmental variables that may drive kelp species distribution.

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Appendix A1: Maxent outputs relating to habitat suitability modelling process for *Ecklonia maxima*.

Table 1. Variable importance to *E. maxima* habitat suitability model, after initial model run with all 23 environmental variables.

Variable	Percent contribution (%)	Permutation importance (%)
cloudmax	38.8*	0
chlomax	16.4*	0
sstmean	9.8*	0.3
parmax	8.9	0
damax	6.4	0
damean	5.9	1.3
damin	5.3	1.3
sstmax	2	0
salinity	1.8	0
sstrange	1.8	41.9**
cloudmin	1.8	0
chlomean	0.2	0
sstmin	0.2	50.4*
nitrate	0.2	0
calcite	0.1	0.1
silicate	0.1	0
ph	0.1	4.7
chlomin	0.1	0
phos	0	0
parmean	0	0
cloudmean	0	0
chlorange	0	0
dissox	0	0

*Variables with the greatest importance to the final habitat suitability model

**Variable accounted for in SSTmin and SSTmax, therefore was not used. SST range did not provide unique information to the model.

Figure 1. Jackknife from final modelling step of *E. maxima* showing variable importance to final habitat suitability model.

Appendix A2: Maxent outputs relating to habitat suitability modelling process for *Ecklonia radiata*.

Table 2. Variable importance to *E. radiata* habitat suitability model, after initial model run with all 23 environmental variables.

Variable	Percent contribution (%)	Permutation importance (%)
cloudmax	31.5*	3.9
chlomin	19.4*	12.8*
calcite	19.3*	0.1
sstmax	9.2	0.9
phos	4.2	69*
chlomax	3.9	0
sstmin	3.3	0
cloudmean	2.8	2.9
silicate	2.2	0
ph	1.5	0.7
parmean	1.3	7.5
sstrange	0.9	0.7
chlorange	0.2	0.1
dissox	0.1	1.1
nitrate	0	0.2
parmax	0	0.1
damean	0	0.1
damin	0	0
salinity	0	0
damax	0	0
cloudmin	0	0
chlomean	0	0
sstmean	0	0

*Variables with the greatest importance to the final habitat suitability model
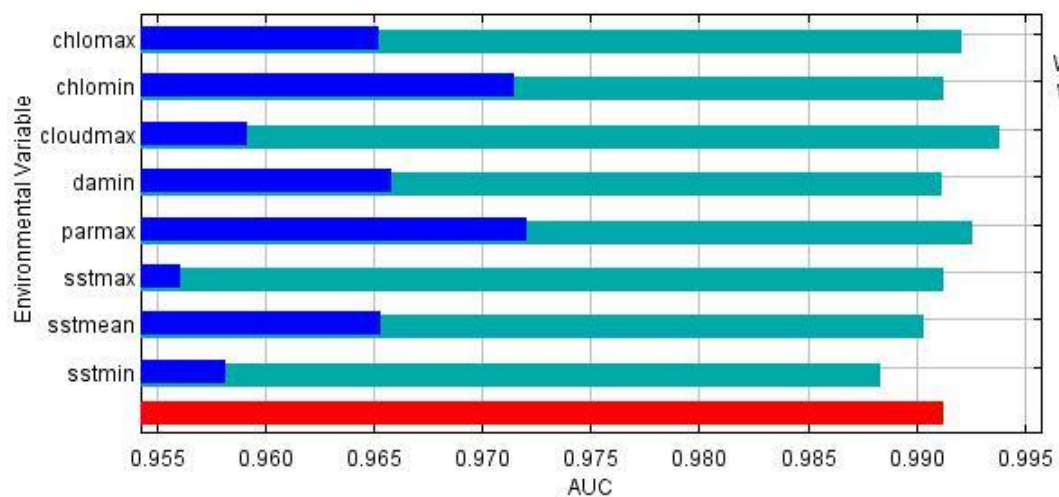
Figure 2. Jackknife from final modelling step of *E. radiata* showing variable importance to final habitat suitability model.

Appendix A3: Maxent outputs relating to habitat suitability modelling process for _Ecklonia cava_.

Table 3. Variable importance to _E. cava_ habitat suitability model, after initial model run with all 23 environmental variables.

Variable	Percent contribution (%)	Permutation importance (%)
sstrange	36*	0
sstmin	17.2*	0
chlomin	17*	0.2
silicate	10.9*	0.2
parmax	8	1.9
nitrate	6	0
cloudmean	2.1	1.3
sstmax	1.1	64.5*
calcite	0.7	0.2
parmean	0.6	30.8*
phos	0.2	0.1
dissox	0.1	0.7
sstmean	0.1	0
chlorange	0.1	0
chlomean	0	0
cloudmax	0	0
chlomax	0	0
ph	0	0
damin	0	0
damean	0	0
damax	0	0
cloudmin	0	0
salinity	0	0

*Variables with the greatest importance to the final habitat suitability model

Figure 3. Jackknife from final modelling step of *E. cava* showing variable importance to final habitat suitability model.

Table 4. Variable importance to *L. pallida* habitat suitability model, after initial model run with all 23 environmental variables

Variable	Percent contribution (%)	Permutation importance (%)
damax	31.9*	1.5
parmax	29.5*	4.3
sstmax	10.2*	0
cloudmax	9.7	0.2
phos	5.1	1.5
salinity	5	0.3
sstrange	3.2	0
cloudmean	2.6	0
sstmean	1.4	57.1*
silicate	0.8	0
sstmin	0.4	34.9*
nitrate	0.1	0
ph	0.1	0.3
parmean	0	0
dissox	0	0
damin	0	0
damean	0	0
cloudmin	0	0
chlorange	0	0
chlomin	0	0
chlomean	0	0
chlomax	0	0
calcite	0	0

*Variables with the greatest importance to the final habitat suitability model
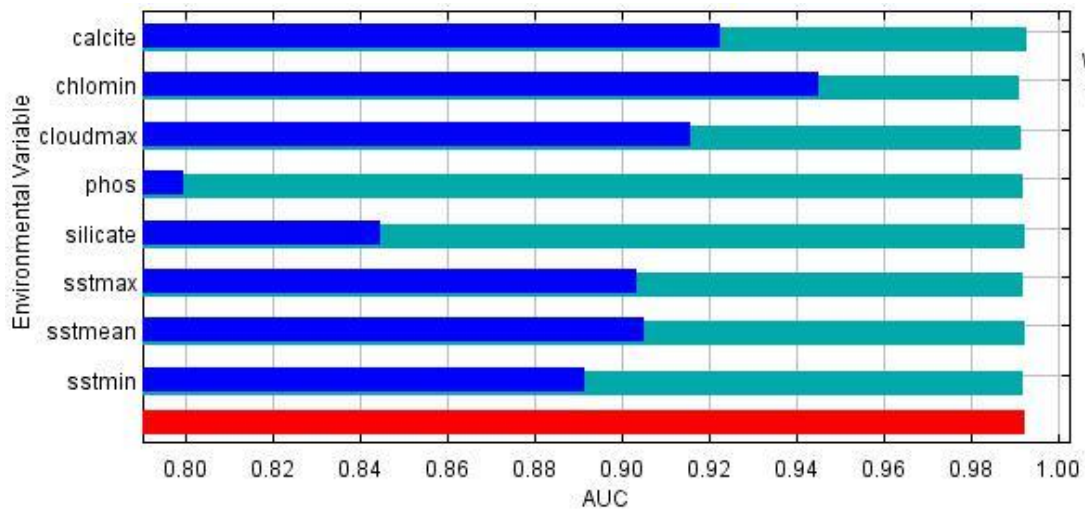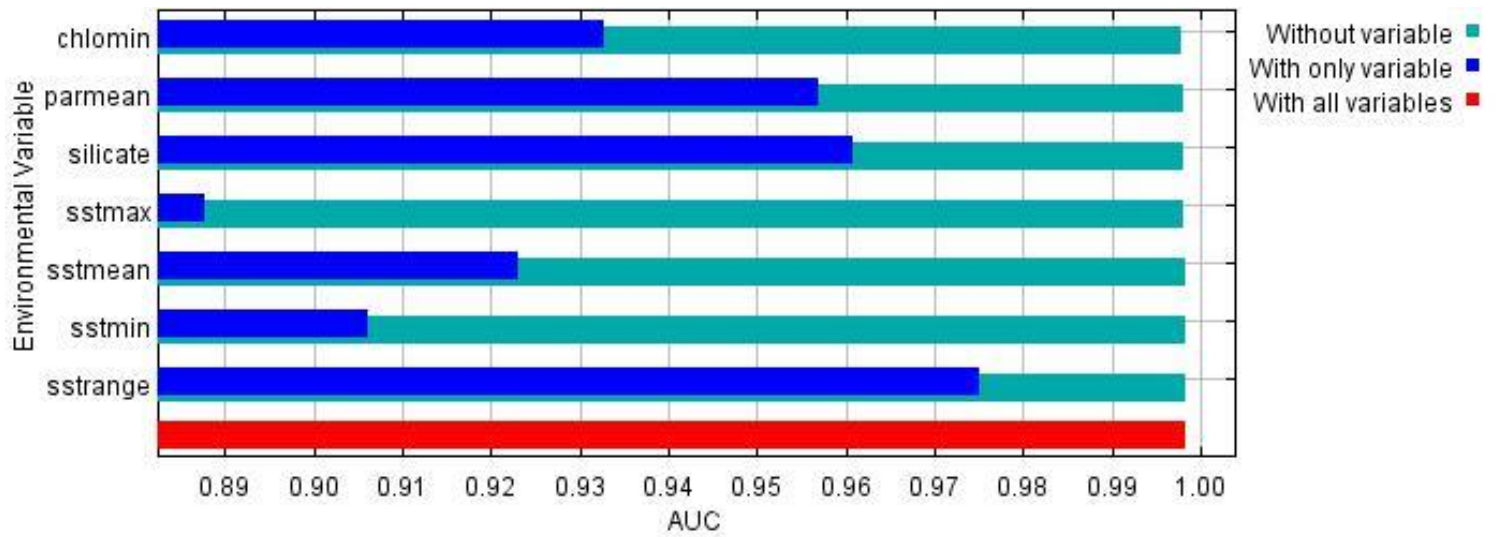
Figure 4. Jackknife from final modelling step of *L. pallida* showing variable importance to final habitat suitability model.

Appendix A5: Maxent outputs relating to habitat suitability modelling process for *L. ochroleuca*.

Table 5. Variable importance to *L. ochroleuca* habitat suitability model, after initial model run with all 23 environmental variables

Variable	Percent contribution (%)	Permutation importance (%)
calcite	45.9*	0.2
silicate	13.3*	0
sstmin	9.6*	0
chlomin	8.7	1.3
sstmax	6.5	0.1
sstmean	5.7	4.4
chlomean	4.1	0
cloudmean	2.5	0.6
phos	1.8	90.2*
nitrate	0.6	0.4
salinity	0.6	2.6
parmax	0.5	0
damin	0.1	0
parmean	0.1	0.1
sstrange	0	0
cloudmax	0	0
chlorange	0	0
dissox	0	0
ph	0	0
damean	0	0
cloudmin	0	0
chlomax	0	0
damax	0	0

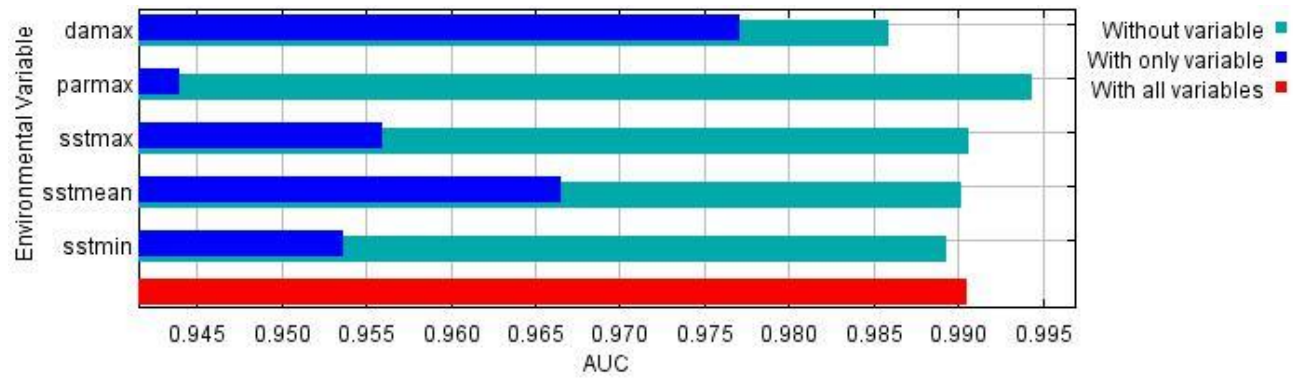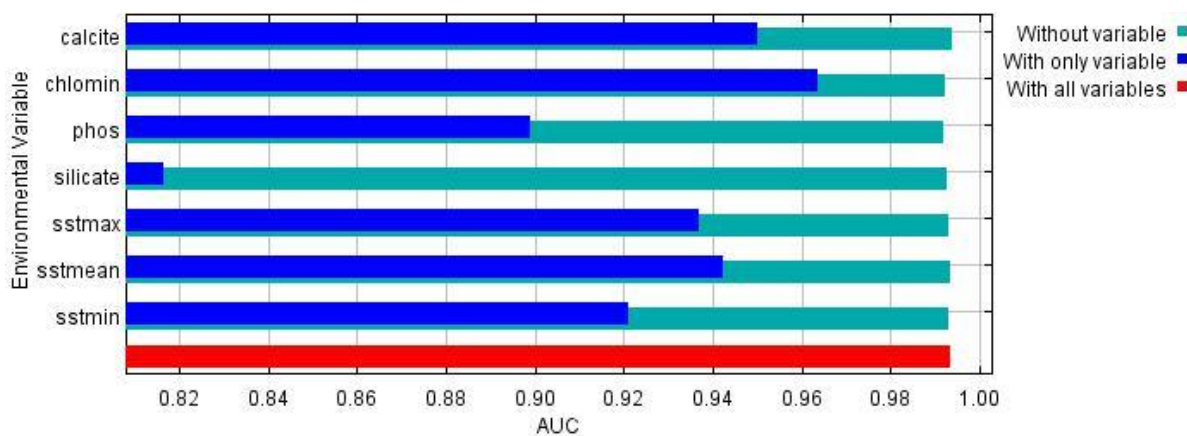*Variables with the greatest importance to the final habitat suitability model

Figure 5. Jackknife from final modelling step of *Laminaria ochroleuca* showing variable importance to final habitat suitability model.

Appendix B: Bio-ORACLE Data represented as maps of global trends in the marine environment.
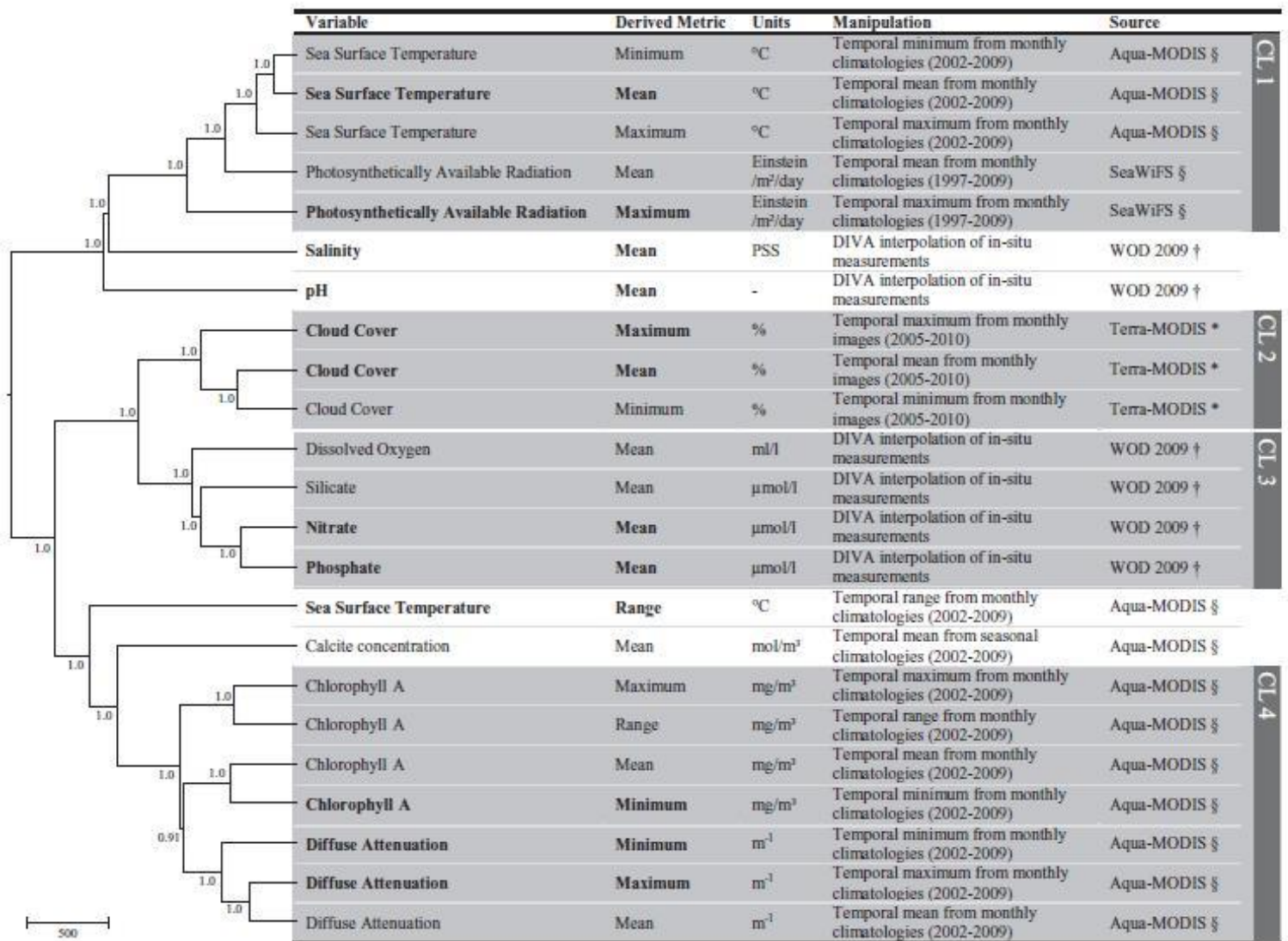

Variable	Derived Metric	Units	Manipulation	Source	
Sea Surface Temperature	Minimum	°C	Temporal minimum from monthly climatologies (2002-2009)	Aqua-MODIS §	CL.1
Sea Surface Temperature	**Mean**	°C	Temporal mean from monthly climatologies (2002-2009)	Aqua-MODIS §	
Sea Surface Temperature	Maximum	°C	Temporal maximum from monthly climatologies (2002-2009)	Aqua-MODIS §	
Photosynthetically Available Radiation	Mean	Einstein /m²/day	Temporal mean from monthly climatologies (1997-2009)	SeaWiFS §	
Photosynthetically Available Radiation	**Maximum**	Einstein /m²/day	Temporal maximum from monthly climatologies (1997-2009)	SeaWiFS §	
Salinity	**Mean**	PSS	DIVA interpolation of in-situ measurements	WOD 2009 †	
pH	**Mean**	-	DIVA interpolation of in-situ measurements	WOD 2009 †	
Cloud Cover	**Maximum**	%	Temporal maximum from monthly images (2005-2010)	Terra-MODIS *	CL.2
Cloud Cover	**Mean**	%	Temporal mean from monthly images (2005-2010)	Terra-MODIS *	
Cloud Cover	Minimum	%	Temporal minimum from monthly images (2005-2010)	Terra-MODIS *	
Dissolved Oxygen	Mean	ml/l	DIVA interpolation of in-situ measurements	WOD 2009 †	CL.3
Silicate	Mean	µmol/l	DIVA interpolation of in-situ measurements	WOD 2009 †	
Nitrate	**Mean**	µmol/l	DIVA interpolation of in-situ measurements	WOD 2009 †	
Phosphate	**Mean**	µmol/l	DIVA interpolation of in-situ measurements	WOD 2009 †	
Sea Surface Temperature	**Range**	°C	Temporal range from monthly climatologies (2002-2009)	Aqua-MODIS §	
Calcite concentration	Mean	mol/m³	Temporal mean from seasonal climatologies (2002-2009)	Aqua-MODIS §	
Chlorophyll A	Maximum	mg/m³	Temporal maximum from monthly climatologies (2002-2009)	Aqua-MODIS §	CL.4
Chlorophyll A	Range	mg/m³	Temporal range from monthly climatologies (2002-2009)	Aqua-MODIS §	
Chlorophyll A	Mean	mg/m³	Temporal mean from monthly climatologies (2002-2009)	Aqua-MODIS §	
Chlorophyll A	**Minimum**	mg/m³	Temporal minimum from monthly climatologies (2002-2009)	Aqua-MODIS §	
Diffuse Attenuation	**Minimum**	m⁻¹	Temporal minimum from monthly climatologies (2002-2009)	Aqua-MODIS §	
Diffuse Attenuation	**Maximum**	m⁻¹	Temporal maximum from monthly climatologies (2002-2009)	Aqua-MODIS §	
Diffuse Attenuation	Mean	m⁻¹	Temporal mean from monthly climatologies (2002-2009)	Aqua-MODIS §	

Figure 6. Bio-ORACLE marine environmental data rasters showing original data sources (Tyberghein et al. 2012).
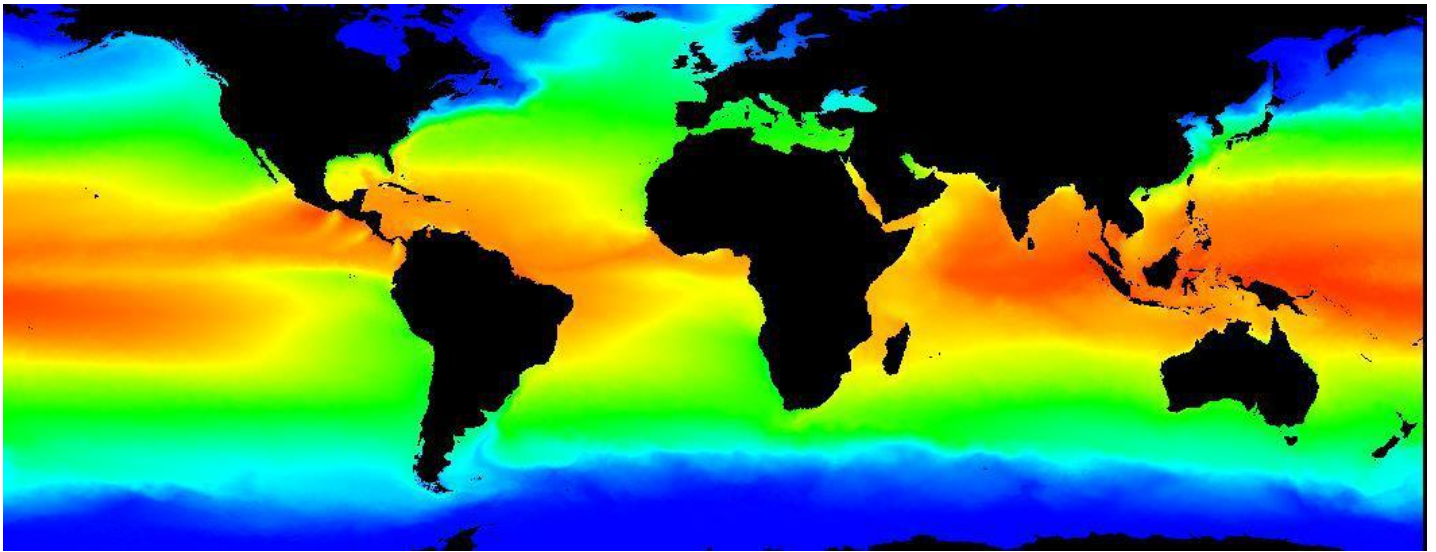
Figure 7. Global map of monthly minimum SST for 2002-2009 taken from satellite data. Warmer colours indicate higher temperatures. (Data Source: Aqua-MODIS)
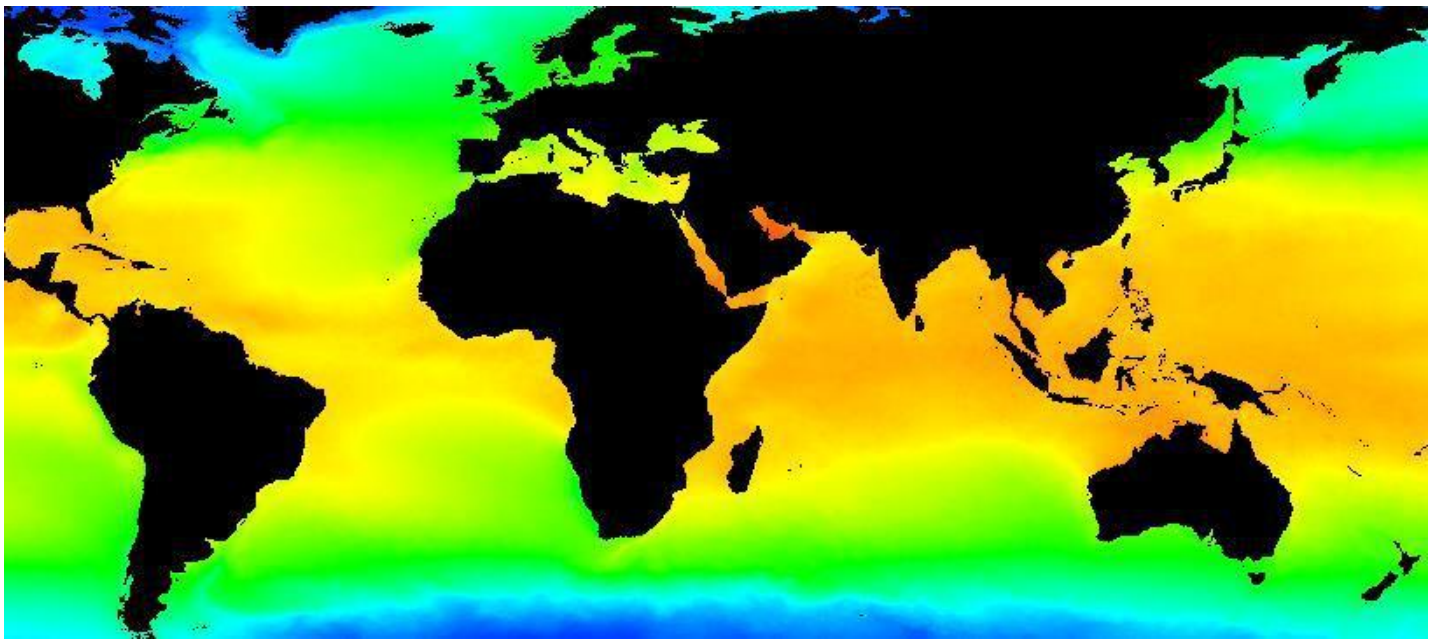

Figure 8. Global map of monthly maximum SST for 2002-2009, from satellite data. Warmer colours indicate higher temperature. (Data Source: Aqua-MODIS)
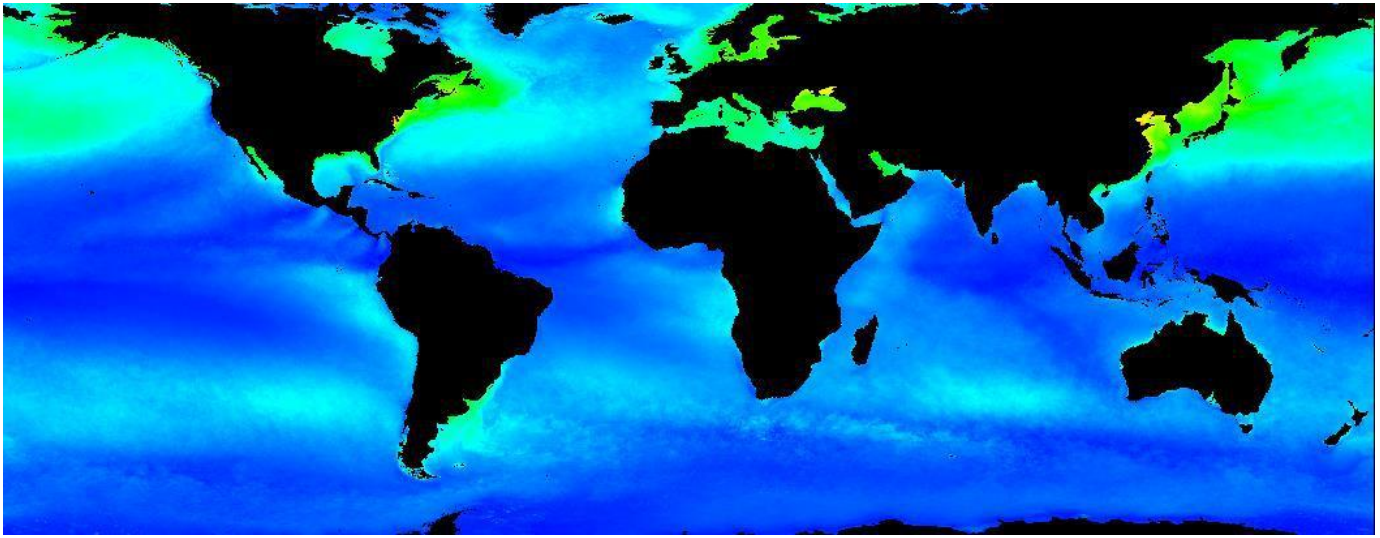
Figure 9. Global map of monthly SST range for 2002-2009, from satellite data. Light blue and green represent high SST range, dark blue denotes low SST range. (Data Source: Aqua-MODIS)
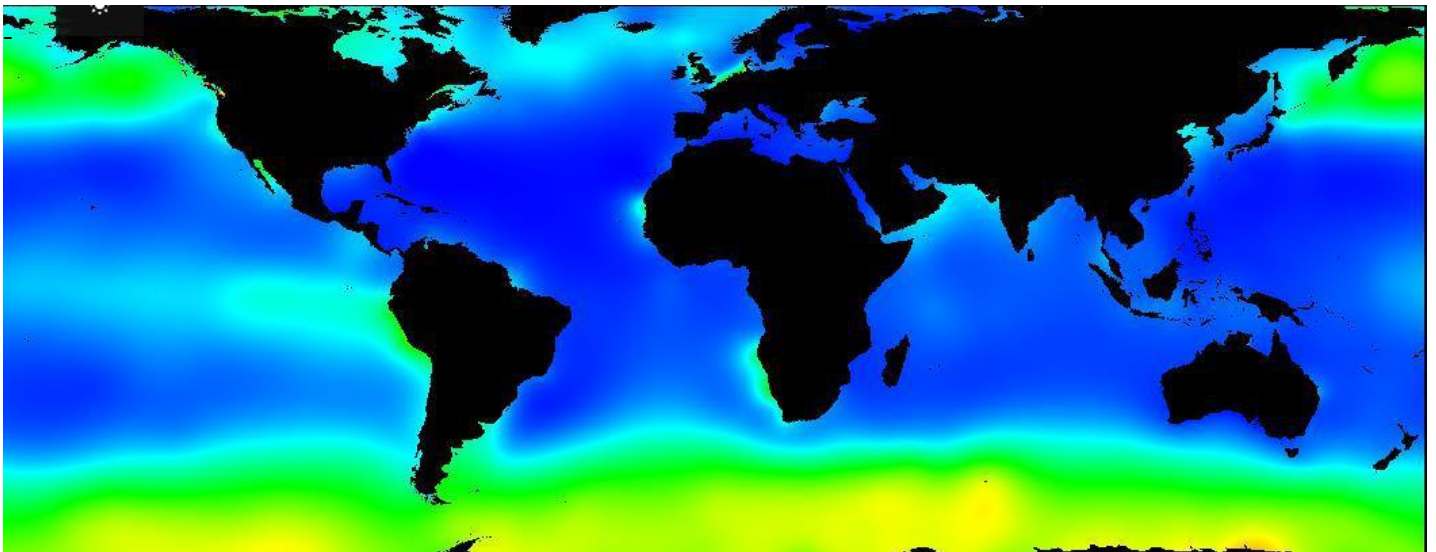

Figure 10. Global map of mean phosphate levels, from *in -situ* data. Yellow, green and light blue indicates higher phosphate levels, dark blue represents low phosphate levels. (Data Source: WOD 2009)
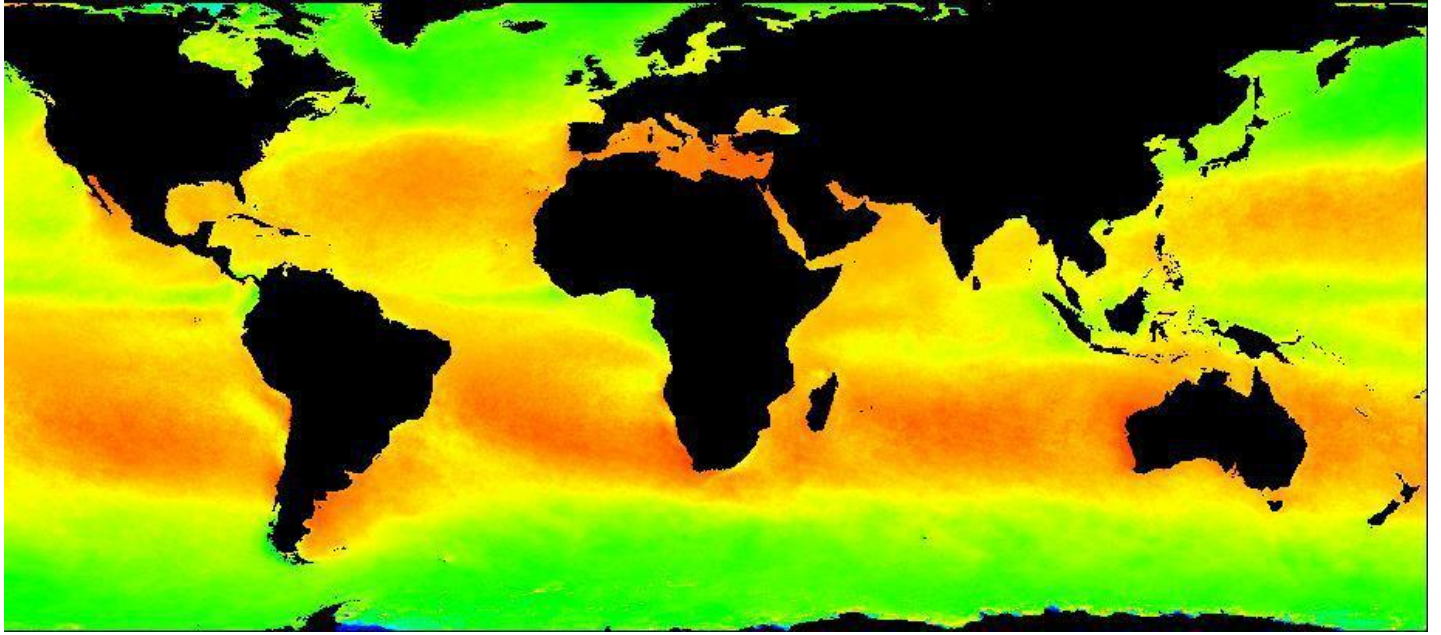
Figure 11. Global map of monthly maximum PAR for 1997-2009, from satellite data. Green shows high PAR and red represents low PAR. (Data Source: Sea-WiFs)
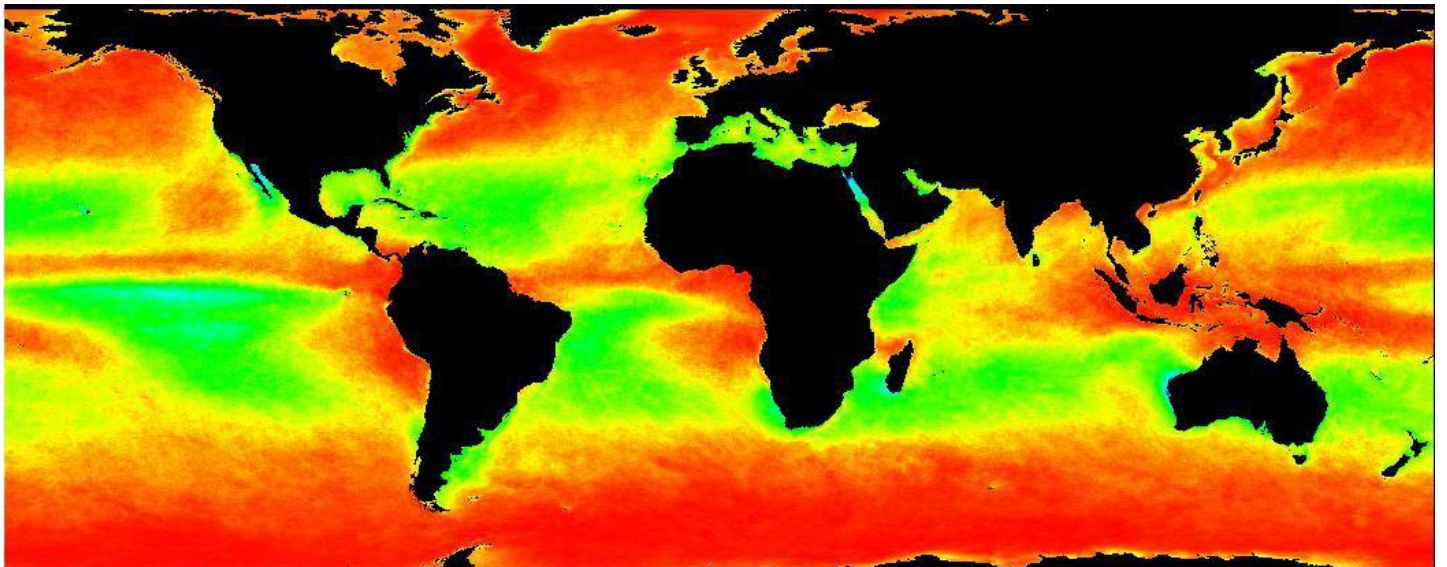

Figure 12. Global map of monthly maximum cloud cover from monthly images for 2005-2010. Red indicates high cloud cover, green indicates low cloud cover. (Data Source: Tera-MODIS)
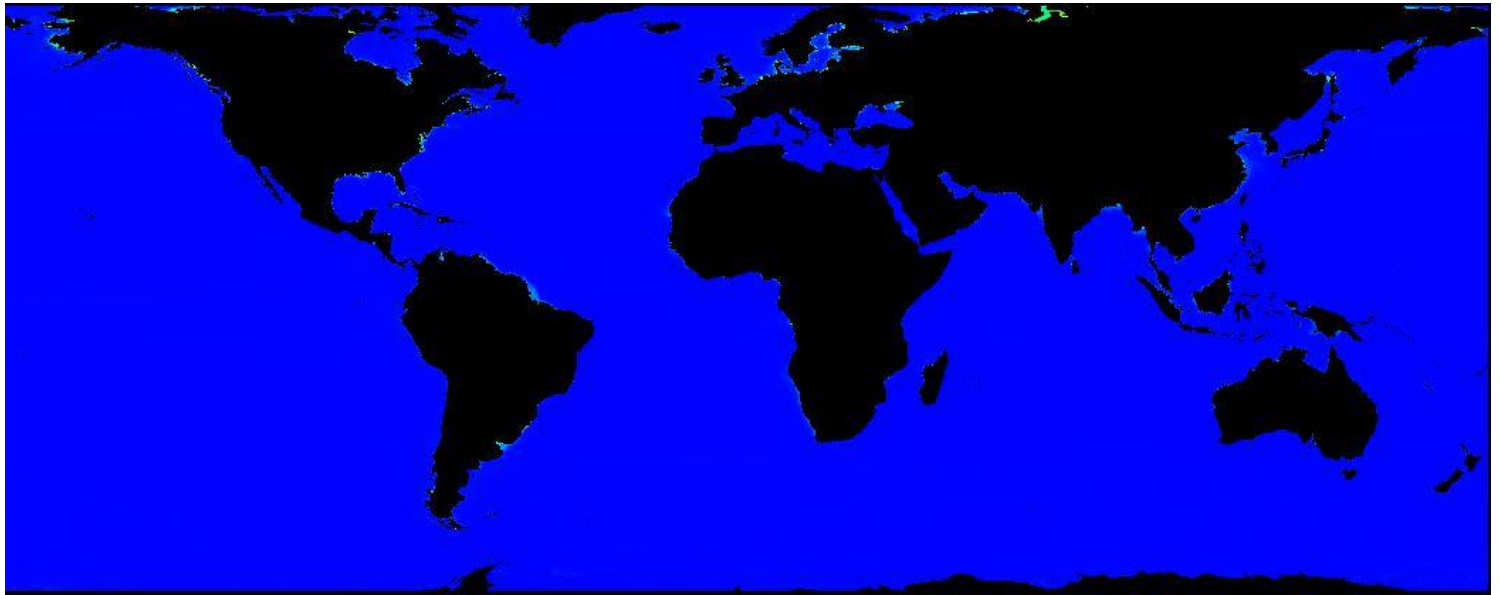
Figure 13. Global map of monthly minimum chlorophyll for 2002-2009, from satellite data. (Data Source: Aqua-MODIS)
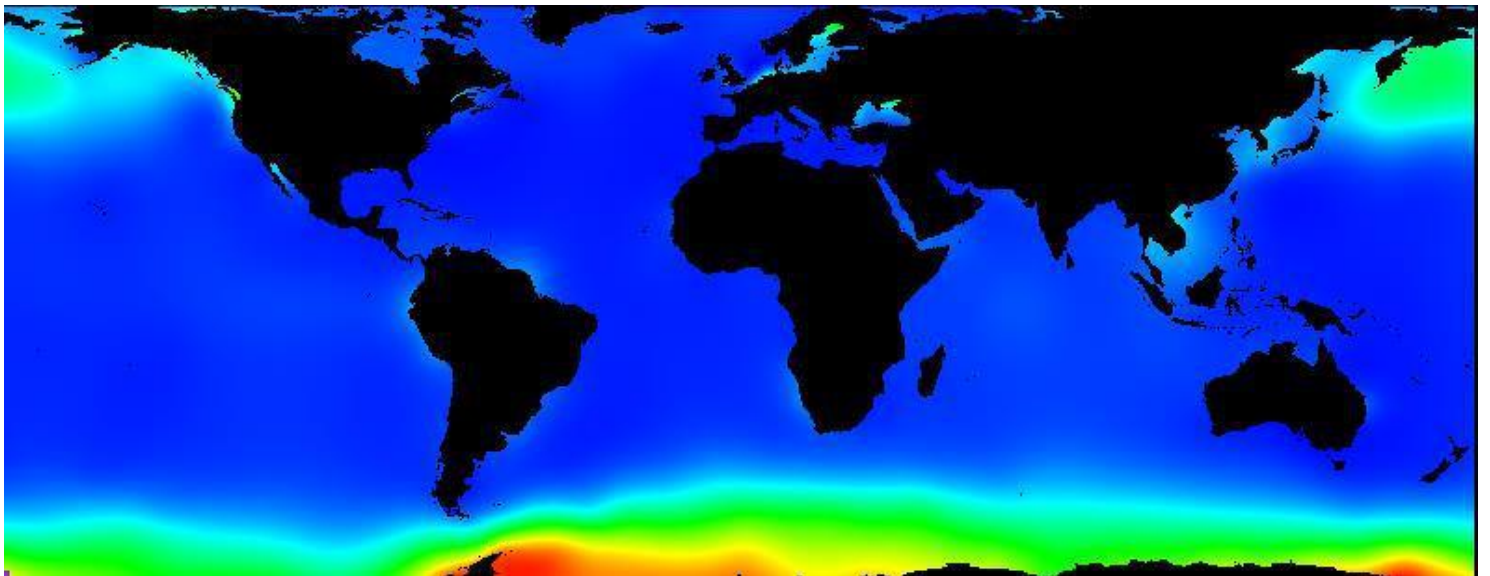

Figure 14. Global map of monthly mean silicate, from *in situ* data.(Data Source: WOD 2009)
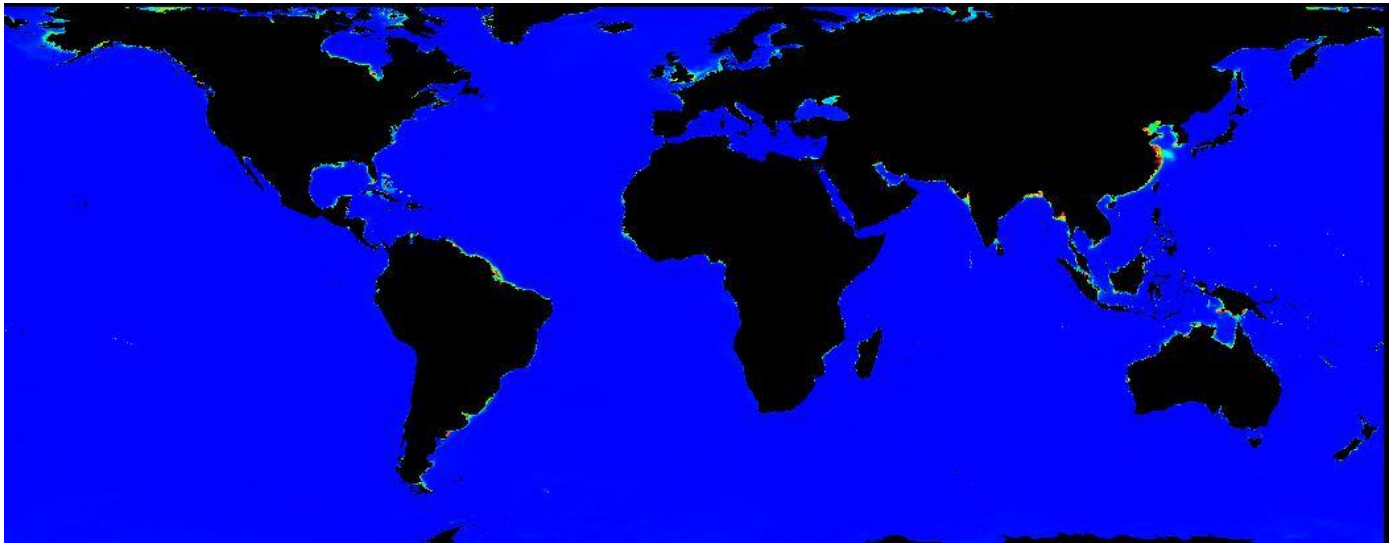
Figure 15. Global map of monthly mean calcite for 2002- 2009, from satellite data.(Data Source: Aqua-MODIS)

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