



Global warming assessment suggests the endemic Brazilian kelp beds to be an endangered ecosystem



A.B. Anderson ^{a,*}, J. Assis ^b, M.B. Batista ^c, E.A. Serrão ^b, H.C. Guabiroba ^a, S.D.T. Delfino ^a, H. T. Pinheiro ^d, C.R. Pimentel ^a, L.E.O. Gomes ^e, C.C. Vilar ^a, A.F. Bernardino ^e, P. Horta ^c, R. D. Ghisolfi ^f, J.-C. Joyeux ^a

^a Laboratory of Ichthyology, Department of Oceanography, Federal University of Espírito Santo, Vitória, ES, 29075-910, Brazil

^b Centre of Marine Sciences, CCMAR, University of Algarve, Campus de Gambelas, 8005-139, Faro, Portugal

^c Laboratório de Ficologia, Departamento de Botânica, Universidade Federal de Santa Catarina, Florianópolis, SC, 88040-970, Brazil

^d Ichthyology Section, California Academy of Sciences, San Francisco, CA, 94118, USA

^e Benthic Ecology Group, Department of Oceanography, Federal University of Espírito Santo, Vitória, ES, 29075-910, Brazil

^f Laboratory of Oceanography, Department of Oceanography, Federal University of Espírito Santo, Vitória, ES, 29075-910, Brazil

ARTICLE INFO

Keywords:
 Anthropocene
 Global warming
 Conservation
 Endemic species
 Endangered species
 Laminariales
 Niche modeling

ABSTRACT

Kelps are canopy-forming brown seaweed sustaining critical ecosystem services in coastal habitats, including shelter, nursery grounds, and providing food resources to a myriad of associated species. This study modeled the fundamental niche of *Laminaria abyssalis* along the Brazilian continental margin, an endemic species of the South Atlantic, to anticipate potential distributional range shifts under two contrasting scenarios of future environmental changes (RCP2.6 and RCP8.5). The model for fundamental niche predictions considering the “present scenario” has shown a wider potential area than the realized niche (i.e., the area where the species actually occurs) along the Brazilian coast. In both future scenarios, the models have shown niche erosion on the northern portion of the Brazilian coast and niche gains towards the south. In both scenarios, *L. abyssalis* populations tend to shift to deeper regions of the reef. The restricted range of occurrence (33,000 km²), intense anthropic activities along these beds (e.g., trawling fisheries, oil/gas mining, or removal for agricultural purposes) acting synergically with global warming, may drive this ecosystem to collapse faster than kelp species’ ability to adapt. We propose to classify *L. abyssalis* as Endangered - (EN) under IUCN criteria, and highlight that long-term monitoring of kelp beds is an urgent need to develop effective conservation initiatives to protect such rare and invaluable ecosystem.

1. Introduction

Biodiversity loss and the global redistribution of marine species have been studied and debated with great concern (Batista et al., 2018; Vergés et al., 2019; Wernberg et al., 2016). Despite all controversy surrounding the “biodiversity shifts and erosion” debate, the great majority of scientists agree that human civilization is responsible, and will be affected directly by global warming (e.g., loss of essential ecological services) (Casado et al., 2019; Morrison et al., 2020; Smale et al., 2019). Concerned scientists are reporting the rapid advance of climate change and its detrimental effects on global biota worldwide (e.g., diversity loss, biological invasions, species horizontal and vertical distributional shifts, extinction) (Assis et al., 2016; Batista et al., 2018; Thomsen et al., 2019;

Wernberg et al., 2019).

On a local scale, marine scientists are warning that climate change is increasing the frequency and severity of marine heatwaves (Arafeh-Dalmau et al., 2019; Rogers-Bennett and Catton, 2019; Thomsen et al., 2019). Such localized and abrupt temperature anomalies associated with heatwaves may cause more rapid biological detrimental changes in marine communities and even extinction (Arafeh-Dalmau et al., 2019; Rogers-Bennett and Catton, 2019; Thomsen et al., 2019). According to Arafeh-Dalmau et al. (2019), a recent (2014–2016) extreme heatwave of unprecedented magnitude and duration in the California Current System altered significantly the Baja California marine communities. Arafeh-Dalmau et al. (2019), detected a significant decrease in kelp species’ density with cold affinities (e.g., *Macrocystis pyrifera*) and fish and

* Corresponding author.

E-mail address: aabbiologia@gmail.com (A.B. Anderson).

invertebrates associated with these ecosystems, and the increase in abundance of fish with warmer affinities, and introduced macroalgae.

Worldwide, in the last three decades, scientists have detected an alarming increase in species distributional shifts along with their native range of occurrence, and migrations to deeper reef zones due to global warming (Assis et al., 2016; Buchanan et al., 2019; Pecl et al., 2017; Vergés et al., 2019), which are expected to influence even climate feedback [e.g., changing the proportion of the incident radiation reflected by the planet (albedo)] (Pecl et al., 2017). In addition, distributional shifts can cause alterations in the marine “biological carbon pump” (i.e., sequestration of carbon from the atmosphere by marine organisms such as seagrasses, micro and macroalgae, and rhodoliths), and cause the release of greenhouse gases (Pecl et al., 2017). In this sense, such biota redistribution constitutes a crucial challenge for human society, which depends to survive, directly and indirectly, on several ecological services provided by living organisms (Pecl et al., 2017; Smale et al., 2019; Wernberg et al., 2019).

Through local to global scales, the distribution of species depends upon several eco-physiological traits (e.g., environmental tolerance to natural and anthropogenic stressors, dispersal constraints, and biological interactions with other species) (Pecl et al., 2017; Wernberg et al., 2019). To avoid extinction, organisms must be resilient to survive in a fast-changing environment, relying on their ecological plasticity to move and adapt to novel habitats (Donelson et al., 2019; Pecl et al., 2017; Wernberg et al., 2019). According to Pecl et al. (2017), the impacts of distributional shifts can cause detrimental effects of the same magnitude as the human-mediated introduction of non-native species, regarded worldwide as one of the main drivers of biodiversity loss. In this regard, the conservation and management of Marine Protected Areas (MPAs) are now facing new challenges considering the acceleration of species distributional shifts (Assis et al., 2016; Casado et al., 2019).

Complex ecosystems such as kelp forests are regarded as highly sensitive to anthropogenic climate change (Rogers-Bennett and Catton, 2019; Thomsen et al., 2019). Global warming has been driving rapid changes in kelps distribution, density and abundance globally over the past two decades (Assis et al., 2016; Batista et al., 2018; Pecl et al., 2017; Vergés et al., 2019; Wernberg et al., 2019). Kelps are long-lived canopy-forming brown seaweeds that grow over the seafloor sustaining critical ecosystem services in coastal habitats (e.g., shelter and food to associated species) (Bennett et al., 2016; Casado et al., 2019). Kelp presents a typically competitive dominant growth habit, with some species reaching tens of meters in height (Wernberg et al., 2019). Their fast growth, vast production of biomass, and three-dimensional alteration of their surrounding physical environment characterize them as environmental bio-engineers (Lutchminarayan, 2018; Wernberg et al., 2019).

Laminarian kelp diversity is currently composed of 112 species in 33 genera (Bolton, 2010; Wernberg et al., 2019). In the Arctic and temperate latitudes, both in the North and South hemispheres, kelps dominate approximately 25% of the world's coastlines (Krumhansl et al., 2016; Wernberg et al., 2019). Kelps evolved approximately 100 million years ago in the northern hemisphere and approximately 30 million years ago diversified into current modern species (Silberfeld et al., 2010). The cooler waters of the Japanese coast harbor the Laminarian kelps highest diversity of species and also their putative ancestors (Bolton, 2010). From northern Japan (the origin of Laminarian kelp), species dispersed across the equator via ‘stepping stones’ using deep waters below the permanent thermocline (Graham et al., 2007; Wernberg et al., 2019). Bolton (2010) also claims that there have been another four independent crossings of the equator: three originating in the north and moving towards the south, and one originating in the south and moving northwards. Currently, the diversity of kelps is 300% higher in the northern than in the southern hemisphere (Bolton, 2010; Wernberg et al., 2019).

Considering the Southwestern Atlantic Ocean, only one species of

kelp is known to occur in a very limited area: *Laminaria abyssalis* (Joly and Oliveira Filho, 1967; Oliveira Filho, 1976, 1978). In 1967, Joly A.B. and Oliveira Filho E.C., described two species of Laminarian kelps for the Brazilian coast (*Laminaria abyssalis* and *Laminaria brasiliensis*). In 1978, Oliveira Filho E.C., described the life cycle of *L. brasiliensis*. Thirty-four years later, a taxonomic study revealed that *L. abyssalis* and *L. brasiliensis* are, in fact, only one species: *L. abyssalis* (Marins et al., 2012; Oliveira Filho, 1978). The populations of *L. abyssalis* described for the Brazilian coast are rare and relicts of shallow-water populations that existed during glacial periods of cooler oceanographic climate (Marins et al., 2012, 2014), which originated from northern laminarian populations at ~ 1.34 myr (Rothman et al., 2017). These relict laminarian beds have been found in a small portion of the Brazilian coast, in tropical latitudes, where there are cool-water microhabitats with suitable conditions (e.g., coastal upwellings and deeper cooler water with sufficient light) (Amado-Filho and Pereira-Filho, 2012; Holz et al., 2020; Quége, 1988; Rothman et al., 2017).

The pressure from anthropogenic activities on marine ecosystems has been driving severe changes in kelp distribution and abundance globally (Assis et al., 2018; Batista et al., 2018; Steffen et al., 2011; Wernberg et al., 2019) where fisheries, ocean acidification, and global warming are stressors of huge concern (Buchanan et al., 2019; Casado et al., 2019; Pauly and Zeller, 2016; Pecl et al., 2017; Vergés et al., 2019). Furthermore, kelps forests decline can also affect a wide range of ecosystem services vital to human well-being, such as recreational and commercial fisheries activities, habitat provision for marine species, climate control through carbon storage, nutrient filtering, and coastline protection (Wernberg et al., 2019).

Species distribution models (SDMs) have been applied worldwide to undertake further ecological investigations concerning species distribution (Casado et al., 2019; Philips and Dudík, 2008). SDMs are considered important tools to understand species ecology, biogeography and to manage and design MPAs (Assis et al., 2016; Boavida et al., 2016; Casado et al., 2019; Lutchminarayan, 2018; Philips and Dudík, 2008). Also, independent of the caution to avoid the selection of inappropriate regions, this method is extremely suitable to access how future emission scenarios influence species highly temperature-dependent (Remya et al., 2015), as the endemic Brazilian kelp *L. abyssalis* (Casado et al., 2019; Wernberg et al., 2019; Wilson et al., 2019) which play an important role improving habitat structure and complexity for fish biodiversity and supporting the local fishermen population. In the past five years, trawling fishermen from the Espírito Santo State, central Brazilian coast, has been reporting frequent captures of *L. abyssalis* fragments, or entire individuals as bycatch, pointing towards an escalating trawling activity on the refuge of the endemic Brazilian deep kelp beds (Bourguignon et al., 2018). Questions started to emerge: 1) What is the fundamental niche availability of *L. abyssalis* along the Brazilian coast? 2) How will climate changes impact the distribution of *L. abyssalis* over time? In this sense, the objective of this study was to model the fundamental niche availability for *L. abyssalis* along the Brazilian coast and its responses to climate change.

2. Methods

2.1. Study area and focal species

Our study area encompasses the distribution of *L. abyssalis* along the Brazilian coast, which ranges between the south of the Abrolhos Bank (19°06' S) and Rio de Janeiro state [near Cabo Frio (23°09'S)] (Marins et al., 2014; Quége, 1988). To develop the SDM models and project potential future distributional shifts, the entire range of occurrence has been considered [Fig. 1 (a, b)].

The Brazilian kelp *L. abyssalis* populations inhabit in a very specific biotope, which is characterized by depths ranging from 40 to 120 m, temperatures ranging from 15°C to 19°C, low light intensity (5–8 m $\text{Em}^{-1} \text{ s}^{-1}$) while growing over a substrate formed by nodules of

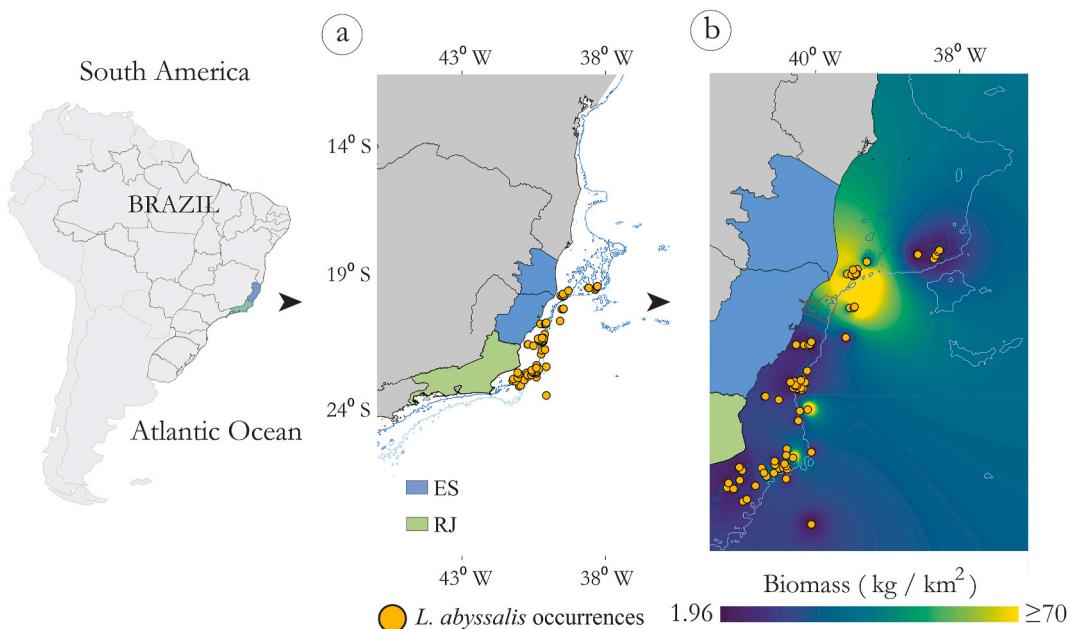


Fig. 1. a) Map of the Brazilian coast showing the limited distribution range of *L. abyssalis*. The orange dots represent the study carried out by Quége (1988), and occurrences found in the literature. The blue box indicates the Espírito Santo State (ES) and the light green box the Rio de Janeiro State (RJ). b) The interpolated map shows the density of *L. abyssalis* in kg/km² according to Quége (1988). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

calcareous algae (rhodolith beds) (Marins et al., 2014; Quége, 1988). In such biotopes, primary production is also directly connected with the occurrence of *L. abyssalis*. The South Atlantic Central Water (SACW) is directly related to the tropical kelp distribution due to its high nitrate (10–15 µM) and phosphate (0.8 µM) concentrations (Marins et al., 2014). Moreover, *L. abyssalis*' populations tend to vary seasonally, within higher productivity during the austral summers (from late December to late March; see Marins et al., 2014).

2.2. Species distribution modeling

The potential distribution of the deep kelp *L. abyssalis* was inferred with ecological niche models using the machine learning algorithm Boosted Regression Trees (BRT). This algorithm fitted climate predictors extracted from Bio-ORACLE (Assis et al., 2018; Tyberghein et al., 2012) against occurrence records (presences and pseudo-absences). The predictors chosen were light at the bottom, nutrients at the bottom (as nitrate and phosphate), salinity at the bottom, the current velocity at the bottom, and sea bottom temperatures (long-term maximum and minimum) which are expected to produce biological meaningful responses for kelp species (Assis et al., 2018; Neiva et al., 2015). Presence records were compiled from literature while pseudo-absences were randomly generated from a probability kernel surface developed with the presence records and a grid with the same resolution of climate data. This step allowed accounting for the spatial bias resulting from an unbalanced distribution of presence records (Assis et al., 2018; Phillips et al., 2009) and also restricting the extent of models to the actual distribution of species (Barve et al., 2011). To further reduce surplus information, the pseudo-absences were climatically structured with a unique membership with K-means clustering, using the number of presence records as the k parameter (Senay et al., 2013).

To reduce the negative effect of spatial autocorrelation (Segurado et al., 2006) the correlation of environmental variables within the range of occurrence records was determined as a function of geographic distance with Mantel tests under 10⁴ permutations (e.g., Boavida et al., 2016). The optimal parameters of the models (i.e., learning rate, tree complexity, and the number of regression trees) were tuned by

implementing a cross-validation framework partitioning the occurrence records (both presences and pseudo-absences) into ten distinct latitudinal bands. This approach assessed performance with AUC (Area Under the Curve) and allowed reducing the effect of overfitting while increasing the potential for temporal/spatial transferability.

2.3. Present and future distributions of *L. abyssalis*

Distribution maps were produced for the present and two distinct future climate scenarios for the year 2100: The Representative Concentration Pathway (RCP) 26 assuming a large reduction of greenhouse gas emissions over time and the RCP 85 characterized by increasing emissions (Moss et al., 2010). All maps were reclassified to binomial surfaces to reflect presence and absences using a threshold maximizing AUC. The loss and gain of potentially suitable habitats were determined for each future climate prediction, both spatially and also through depth.

The final performance of predictions was assessed with AUC, sensitivity (true presence rate), and True Skill Statistics (TSS > 0.8 excellent accuracy) (Allouche et al., 2006). Partial dependence plots were also produced to depict the effect of each climate predictor on the response of models by following the implementation for BRT (Elith et al., 2008).

3. Results

The performance of the models for present times retrieved an excellent description of *L. abyssalis* known distribution (TSS: 0.904, Sensitivity: 1 and AUC: 0.952) (Table 1). The relative contribution of each environmental variable on the accuracy of the models presented herein showed that the niche of *L. abyssalis* is mainly shaped by the light

Table 1

Summary of model performance assessed for the cross-validation and the final predictions.

Model	AUC	Sensitivity	TSS
Cross-validation	0.926 ± 0.107	0.907 ± 0.211	0.853 ± 0.264
Final prediction	0.952	1	0.904

availability at the bottom, temperatures ranging from 15 to 27 °C and ocean currents velocity of 0.17 m/s (Table 2). The present potential distribution of the deep kelp *L. abyssalis* predicted by the BRT algorithm revealed a potential fundamental niche ranging from the Northeast of the Brazilian coast (Bahia state) to Argentina, with a total suitable area of 75,839 km² at optimum depths of 74.20 (± 40.20) meters (Fig. 2, Table 3). Considering different Representative Concentration Pathways (RCPs) future (2090–2100) scenarios: RCP 26 (assuming a large reduction of greenhouse gas emissions over time) and RCP 85 (assuming increasing greenhouse gas emissions over time), *L. abyssalis* presented similar responses regarding the losses and gains of suitable habitats in both scenarios (Fig. 2). In RCP 26 future scenario the deep kelp shows fundamental niche erosion for the northern region of the Brazilian coast (Fig. 2) and a total suitable habitat loss of 7838 km² (Table 3). Otherwise, fundamental niche shifts towards the Southern Brazilian coast reaching Uruguay and Argentina, and towards deeper zones, represented a niche availability gain of 47,177 km², at optimum depths at 86.24 (± 37.81) meters (Fig. 2, Table 3). In RCP 85 future scenario *L. abyssalis* shows prominent fundamental niche erosion on the northern portion of the Brazilian coast within shifts towards the Southern Brazilian coast reaching Uruguay and Argentina; a suitable habitat loss of 28,780 km², and a poleward gain of 56,394 km². The suitable depths in RCP 85 scenario shifted to 99.09 (± 33.33) meters (Fig. 3, Table 3).

4. Discussion

The model response for the endemic Brazilian kelp *L. abyssalis* was mainly shaped by light availability at the bottom, temperatures ranging from 15 to 27 °C and ocean currents velocity (Table 2); which results in a predicted present potential distribution (i.e., fundamental niche) to an area much larger than actually known, as those with Southeast Brazil [the richest part of the Brazilian coast, and most highly populated and heavily fished; Figs. 1 (a), Fig. 2 (a) and Fig. 4; IBGE, 2013; Vasconcellos and Gasalla, 2001]. These results support that the Brazilian endemic kelp *L. abyssalis* realized niche is limited to the transition zone between the “Tropical” (i.e., the northern portion of the Brazilian coast) and the “Warm temperate” biogeographic sub-provinces (see Carvalho et al., 2020; Quége, 1988).

The Costa das Algas MPA is a region prone to the intrusion of colder and nutrient-enriched water at the bottom of the continental shelf (Palóczy et al., 2016). There, Ekman pumping (e.g., Castelao and Barth, 2006), and encroachment (e.g., Aguiar et al., 2014) are likely to bring thermocline water onto the continental shelf. Similar specific environmental conditions have been described for the congener kelp *L. rodiguezii* in the Mediterranean Sea (Žuljević et al., 2016). According to Žuljević et al. (2016), Mediterranean unidirectional currents and the presence of rhodolith beds play a very important role in the occurrence of *L. rodiguezii*.

Despite the larger fundamental niche available predicted by the model, such specific conditions represent a limited area of occurrence for the endemic Brazilian deep kelp (Fig. 2). Large Brazilian kelp beds (i.e., 300 kg/km²) have been registered, so far, only for the northern portion of the coast of Espírito Santo State, near the Doce River Shelf (Fig. 1) (Amado-Filho et al., 2007; Amado-Filho and Pereira-Filho, 2012; Holz et al., 2020; Quége, 1988).

Table 2
Variable percentage contribution to the models and inferred limiting point (L).

Variable	Contribution (%)	L. point
Light at bottom	31.04	$2.15 \text{ e}^{-5} \text{ E. m}^{-2} \text{ yr}^{-1}$
Max. Ocean temp.	21.36	26.92 °C
Current velocity	19.03	0.17 m/s
Min. Ocean temp.	17.65	15.25 °C
Phosphate	6.08	$2.47 \text{ e}^{-2} \text{ mmol. M}^{-3}$
Nitrate	4.81	$1.76 \text{ e}^{-4} \text{ mmol. M}^{-3}$
Salinity	0	—

The restricted distribution of *L. abyssalis* beds reveals a species with high habitat affinity [i.e., right temperature, right depth, good water transparency, dim light, right current direction and velocity, and the right concentration of nutrients (upwellings)] (Table 2) (Marins et al., 2014; Quége, 1988; Rodrigues et al., 2002; Yoneshigue-Valentin, 2012; Žuljević et al., 2016). Such habitat dependency can be posing a threat to *L. abyssalis* beds, once the region is heavily exploited by artisanal and industrial fisheries (mostly shrimp trawlers) and the oil industry (ANP, 2020; IBGE, 2013).

In both RCP scenarios (greenhouse gas emissions decrease and increase) we detected distributional range gains towards the south and deeper zones of the reef, and losses on the northern portion of the Brazilian coast (Fig. 2); which reinforce that ongoing and future global warming has the potential to produce distributional shifts of kelp (Casado et al., 2019). If the worst-case scenario is taken into account (RCP85/2100), patterns of range erosion on the northern portion of the coast, distributional shifts towards the south, and deeper zones of the reef become clearer (Figs. 2 and 3). According to Casado et al. (2019), in the past three decades, the effective niche of seven of the most conspicuous seaweeds of the Iberian Peninsula has contracted. Declines in the area of kelp forests have been observed in long-timescale studies (30–50 years) in Nova Scotia, the Gulf of Maine, North-Central California, Norway, Ireland, and South Australia, where some of the longest available time series of kelp abundances exist (Wernberg et al., 2019). Despite the gains and population shifts towards the south and deeper reef zones of the Brazilian coast, variables such as physiological plasticity and adaptation to rapid environmental change were not considered (see Wilson et al., 2019). Kelps are temperature-dependent organisms for which growth and photosynthesis are compromised when temperatures differ from the “optimum” (Casado et al., 2019; Wernberg et al., 2019; Wilson et al., 2019). As studies worldwide warn about the continuous increase in seawater temperature and state that temperature is the most relevant threat to canopy-forming algae, one may regard the future of kelps with great concern (Batista et al., 2018; Casado et al., 2019; Wernberg et al., 2019; Wilson et al., 2019). Climate change may occur at faster rates than predicted, impeding species to migrate to novel habitats (Assis et al., 2018; Wilson et al., 2019). Additionally, stronger and more frequent heatwaves detected worldwide can accelerate climate change impacts dramatically on marine communities (Arafeh-Dalmau et al., 2019; Filbee-Dexter et al., 2020; Rogers-Bennett and Catton, 2019; Smale et al., 2019; Thomsen et al., 2019). Instead of adapting to a rapidly changing world through distributional shifts and depth shifts, rare endemic species with high habitat affinities, occurring in highly populated and overexploited areas, such as the Brazilian deep kelp *L. abyssalis*, may be doomed to extinction. Thomsen et al. (2019) reported the local extinction of the Bull kelp (*Durvillaea* spp.) due to a strong marine heatwave, in the rocky intertidal zone on the east coast of the South Island of New Zealand. According to Assis et al. (2018), some species of kelps are climatic relicts at threat of disappearing; such changes worldwide are leading to profound impacts on the global economy, food supply, and health (Vergés et al., 2019).

According to Quége (1988), the endemic Brazilian deep kelp beds occurs in a very small area with a low biomass average per km² (i.e., average 65.40 kg/km² per 33,000 km² total occurrence area), and densest populations (~ 300 kg/km²) are located on the Doce River shelf, in the northern portion of Espírito Santo State (Figs. 1 and 4). The region harbors also, portions of the largest rhodolith beds in the world (Holz et al., 2020), and is considered a transitional ecoregion (Carvalho et al., 2020; Horta et al., 2001), with the richest marine fish and benthic diversity along the Brazilian coast (Aued et al., 2018; Floeter et al., 2008; Holz et al., 2020). The area has been impacted by successive catastrophic environmental disasters since 2015 (Carmo et al., 2017; Escobar, 2019; Gomes et al., 2017; Holz et al., 2020; Magris and Giarrizzo, 2020; Queiroz et al., 2018). On November 5th, 2015, the Samarco's Fundão iron mining tailings dam collapsed releasing ~ 35 to 50 million m³ of toxic mud on the Doce River basin, 600 km inland, characterizing

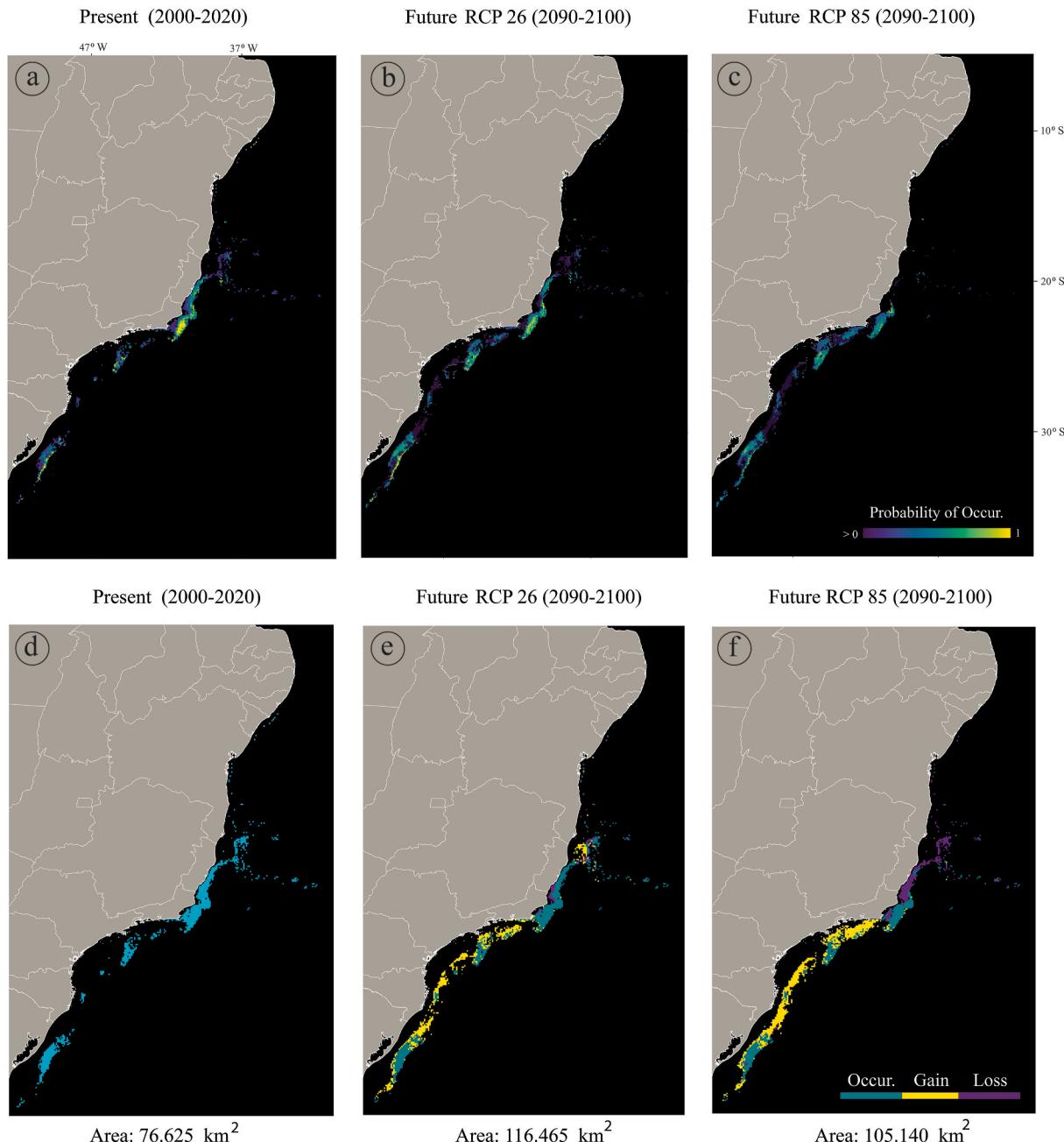


Fig. 2. Predicted potential distribution of *L. abyssalis*. A) Fundamental niche probabilities; B) fundamental niche probabilities in a future (2100-RCP26) global warming scenario; C) fundamental niche probabilities in the future (2100-RCP85) global warming scenario; D) Present total predicted area; E) occurrence, area gain and loss in a future (2100-RCP26) global warming scenario; F) occurrence, gain and loss area in the future (2100-RCP85) global warming scenario.

Table 3

Predicted suitable habitats in terms of area [present and future scenarios RCP26 and RCP 85 (year 2100)], and suitable depths (mean and the 95th percentile of all suitable depths).

Prediction	Total area (km ²)	Area loss (km ²)	Area gain (km ²)	Depth (mean and 95 th percentile)
Present	75,839	–	–	74.20 ± 40.20 [14–160]
RCP26	116,022	7838	47,177	86.24 ± 37.81 [20–162]
RCP85	103,453	28,780	56,394	99.09 ± 33.33 [36–166]

the world's biggest environmental mining disaster in human history (Gomes et al., 2017; Holz et al., 2020; Queiroz et al., 2018). The toxic mud traveled along the Rio Doce river for 17 days reaching the coast through the Rio Doce estuary. The impacts of the toxic mud massive discharge on the Brazilian deep kelp beds, rhodolith beds, and the entire ecosystem are still unknown (Gomes et al., 2017; Holz et al., 2020; Queiroz et al., 2018). In addition, in late August 2019, approximately 400 localities (~3000 km) of the northern and southeastern Brazilian coast have been exposed to hundreds of tons of crude oil and the associated physical and chemical disturbance, the direct consequences on the marine diversity were devastating, the total extent of such impacts is still unknown (Escobar, 2019; Magris and Giarrizzo, 2020).

Considering the increasing rates of disturbances on seabed due to human activities on *L. abyssalis* unique refuge (e.g., bottom trawling

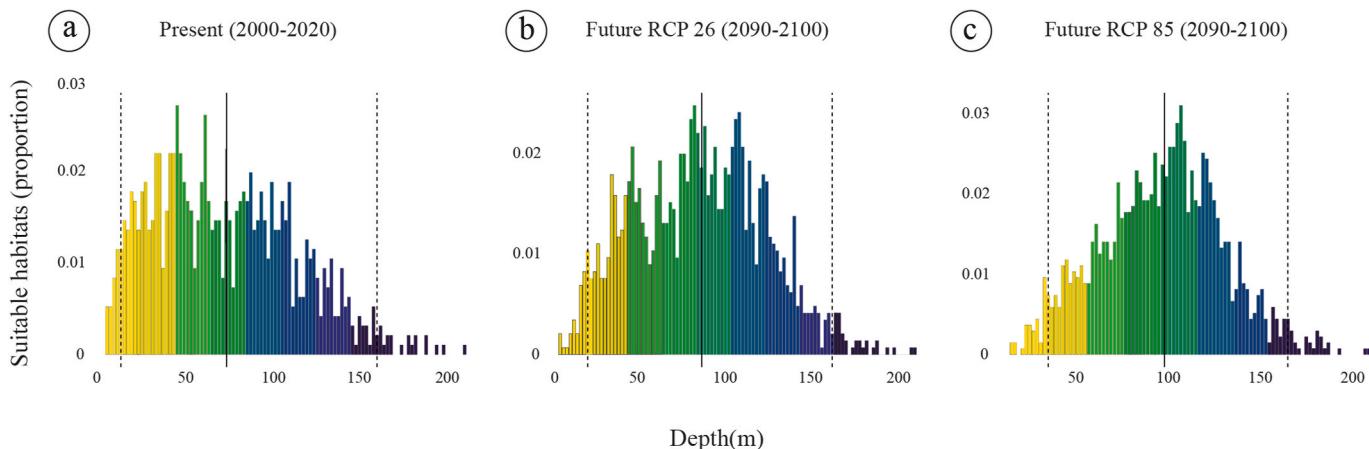


Fig. 3. Predicted vertical distribution of *L. abyssalis*, black line depicts mean predicted suitable depth and dashed lines the 95th percentile of all suitable depths. A) Present model; B) Future model (2100-RCP26) global warming scenario; C) Future model (2100-RCP85) global warming scenario.

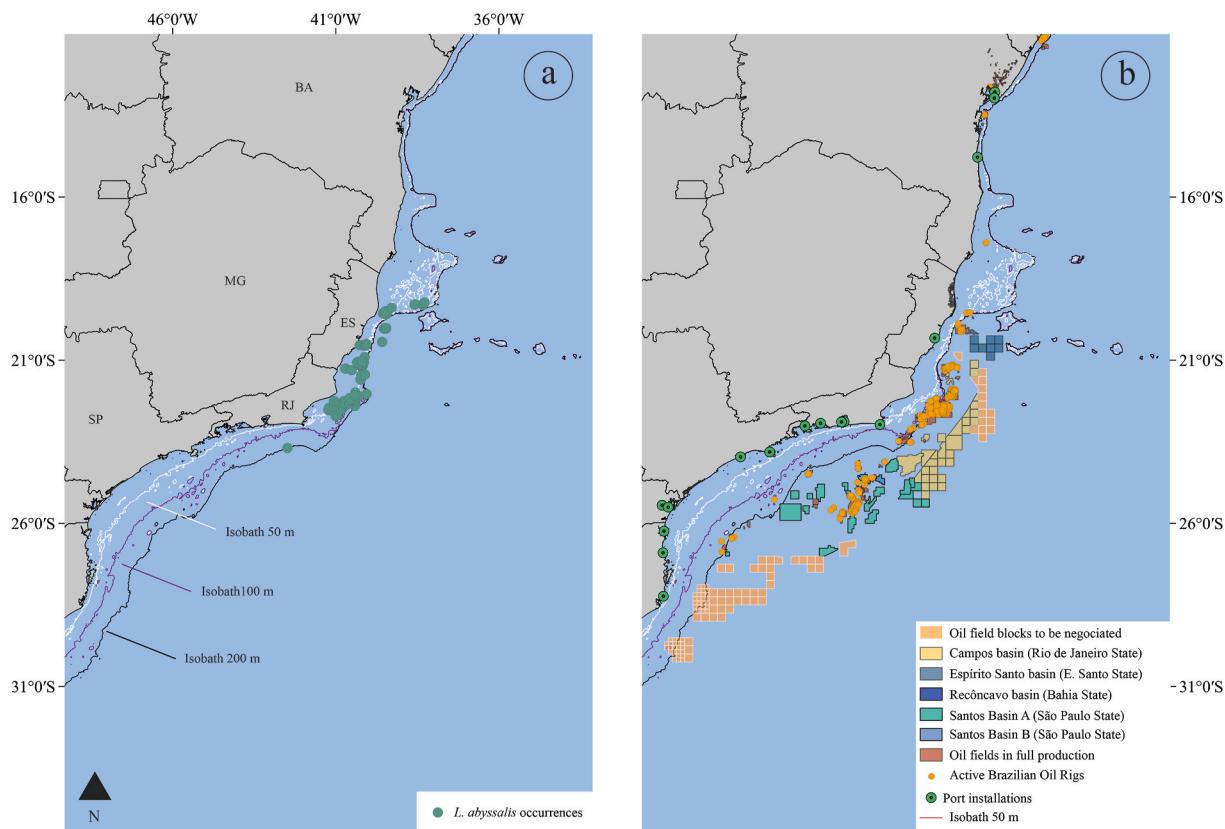


Fig. 4. Maps showing the occurrence area of *L. abyssalis* in the most populated and richest area of the Brazilian coast. a) The restricted range of distribution of *L. abyssalis* between Espírito Santo State (ES) and Rio de Janeiro State (RJ). b) Port activities and oil mining along *L. abyssalis* area of occurrence.

fishery), global warming, ocean acidification, successive and catastrophic environmental impacts in the past five years, we propose that *L. abyssalis* should be classified as endangered (EN) under IUCN criteria: version 3.1. (IUCN, 2012, 2020). According to IUCN criteria, rare endemic species with the geographic localization of the population near human highly populated areas; species with a limited/small range of occurrence; species with seasonal populational fluctuations; species with a projected reduction on its population, can be considered at risk of extinction.

Long-term monitoring programs, molecular studies and conservation initiatives must be encouraged urgently, as proposed for *L. rodiguezii* in Palagruža Island, Adriatic Sea (Žuljević et al., 2016), and Menorca

Channel (Balearic Islands, western Mediterranean) (Barberá et al., 2012). Also, the implementation of a no-entry/no-take marine protected area would reduce trawling activities and allow marine scientists to evaluate the real results of the impacts suffered by *L. abyssalis*, and the diverse biota which dwells in such a unique ecosystem.

5. Conclusions

The present model for Brazilian kelp beds potential distribution (i.e., fundamental niche) has shown a wider area than the realized niche along the Brazilian coast. Future models considering two possible scenarios (RCP 26 and 85) predicted populational niche shifts. Even if a

significant reduction in greenhouse gas emissions (RCP 26) fundamental niche shifts are going to occur, both future scenarios indicate niche erosion on the northern portion of the Brazilian coast and gains towards the south. Also, in both scenarios, *L. abyssalis* populations tend to shift to deeper regions.. The relict endemic Brazilian kelp *L. abyssalis* tends to have similar responses to global warming as other kelp species worldwide. Furthermore, the increase in anthropogenic stressors as trawling activities and environmental catastrophes coupled to global warming scenarios can erode the unique refuge of the Brazilian kelp *L. abyssalis* to extinction. In this sense, effective conservation strategies and research initiatives are crucial to understand the environment and preserve the species.

CRediT authorship contribution statement

A.B. Anderson: Conceptualization, Methodology, Writing – original draft, Writing – review & editing, Formal analysis, preparation, Statistical analyses. **J. Assis:** Writing – review & editing, Formal analysis, Statistical analyses. **M.B. Batista:** Writing – review & editing, Formal analysis, Statistical analyses. **E.A. Serrão:** Writing – review & editing, Formal analysis, Statistical analyses. **H.C. Guabiroba:** Data curation, Writing – review & editing. **S.D.T. Delfino:** Writing – review & editing, Data curation. **H.T. Pinheiro:** Conceptualization, Writing – review & editing. **C.R. Pimentel:** Data curation, Writing – review & editing. **L.E. O. Gomes:** Conceptualization, Writing – review & editing. **C.C. Vilar:** Conceptualization, Writing – review & editing. **A.F. Bernardino:** Writing – review & editing. **P. Horta:** Writing – review & editing. **R.D. Ghisolfi:** Writing – review & editing. **J.-C. Joyeux:** Supervision, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Thanks to FAPES (Fundação de Amparo à Pesquisa e Inovação do Espírito Santo, Brazil), CAPES and CAPES Print (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, Brazil) - PROFIX program Nº 10/2018 - T.O.: 348/2018 for Antônio B. Anderson Postdoctoral scholarship. This study was also supported by a Pew Marine Fellowship (USA) and the Foundation for Science and Technology UID/Multi/04326/2019, PTDC/MAR-EST/6053/2014, SFRH/BSAB/150485/2019, PTDC/BIA-CBI/6515/2020 and the transitional norm - DL57/2016/CP1361/CT0035. L.E.O.G. was supported by a PELD-HCES scholarship. Thanks to PELD-HCES for funding and field support, and ICTIOLAB researchers for field support and partnership. CRP also thanks FAPES for the PhD scholarship and CAPES for the PDSE fellowship. HTP is supported by the Hope for Reefs Initiative of the California Academy of Sciences. PH also thanks CNPq, FAPESC and Fundação Boticário for the financial support.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marenres.2021.105307>.

References

- Aguiar, A.L., Cirano, M., Pereira, J., Marta-Almeida, M., 2014. Upwelling processes along a western boundary current in the Abrolhos-Campos region of Brazil. *Continent Shelf Res.* 85, 42–59.
- Allouche, O., Tsao, A., Kadmon, R., 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *J. Appl. Ecol.* 43, 1223–1232.
- Amado-Filho, G.M., Maneveldt, G., Manso, R., Marins-Rosa, B., Pacheco, M., Guimarães, S., 2007. Structure of rhodolith beds from 4 to 55 meters deep along the southern coast of Espírito Santo State, Brazil. *Cien. Mar.* 33, 399–410.
- Amado-Filho, G.M., Pereira-Filho, G.H., 2012. Rhodolith beds in Brazil: a new potential habitat for marine bioprospection. *Revista Brasileira de Farmacognosia* 22, 782–788.
- ANP, 2020. In: Agência Nacional do Petróleo - Shapefile de Dados. Brazilian Federal Government, Brazil. <http://www.anp.gov.br/exploracao-e-producao-de-oleo-e-gas/dados-tecnicos/shapefile-de-dados>. W.W.e.p.A.f. (Ed.).
- Arafeh-Dalnau, N., Montaño-Moctezuma, G., Martínez, J.A., Beas-Luna, R., Schoeman, D.S., Torres-Moye, G., 2019. Extreme marine heatwaves alter kelp forest community near its equatorward distribution limit. *Front. Mar. Sci.* 6, 499.
- Assis, J., Araújo, M.B., Serrão, E.A., 2018. Projected climate changes threaten ancient refugia of kelp forests in the North Atlantic. *Global Change Biol.* 24, e55–e66.
- Assis, J., Lucas, A.V., Bárbara, I., Serrão, E.A., 2016. Future climate change is predicted to shift long-term persistence zones in the cold-temperate kelp *Laminaria hyperborea*. *Mar. Environ. Res.* 113, 174–182.
- Aued, A.W., Smith, F., Quimbayo, J.P., Cândido, D.V., Longo, G.O., Ferreira, C.E.L., Witman, J.D., Floeter, S.R., Segal, B., 2018. Large-scale patterns of benthic marine communities in the Brazilian Province. *PLoS One* 13, e0198452.
- Barberá, C., Moranta, J., Ordines, F., Ramón, M., de Mesa, A., Díaz-Valdés, M., Grau, A. M., Massuti, E., 2012. Biodiversity and habitat mapping of Menorca Channel (western Mediterranean): implications for conservation. *Biodivers. Conserv.* 21, 701–728.
- Barve, N., Barve, V., Jiménez-Valverde, A., Lira-Noriega, A., Maher, S.P., Peterson, A.T., Soberón, J., Villalobos, F., 2011. The crucial role of the accessible area in ecological niche modeling and species distribution modeling. *Ecol. Model.* 222, 1810–1819.
- Batista, M.B., Anderson, A.B., Franzan Sanches, P., Simionatto Polito, P., Lima Silveira, T., Velez-Rubio, G., Scarabino, F., Camacho, O., Schmitz, C., Martinez, A., 2018. Kelps' long-distance dispersal: role of ecological/oceanographic processes and implications to marine forest conservation. *Diversity* 10, 11.
- Bennett, S., Wernberg, T., Connell, S.D., Hobday, A.J., Johnson, C.R., Poloczanska, E.S., 2016. The 'Great Southern Reef': social, ecological and economic value of Australia's neglected kelp forests. *Mar. Freshw. Res.* 67, 47–56.
- Boavida, J., Assis, J., Silva, I., Serrão, E.A., 2016. Overlooked habitat of a vulnerable gorgonian revealed in the Mediterranean and Eastern Atlantic by ecological niche modelling. *Sci. Rep.* 6, 36460.
- Bolton, J.J., 2010. The biogeography of kelps (Laminariales, Phaeophyceae): a global analysis with new insights from recent advances in molecular phylogenetics. *Helgol. Mar. Res.* 64, 263–279.
- Bourguignon, S.N., Bastos, A.C., Quaresma, V.S., Vieira, F.V., Pinheiro, H., Amado-Filho, G.M., De Moura, R.L., Teixeira, J.B., 2018. Seabed morphology and sedimentary regimes defining fishing grounds along the eastern Brazilian shelf. *Geosciences* 8, 91.
- Buchanan, J.R., Ralph, G.M., Krupp, F., Harwell, H., Abdallah, M., Abdulqader, E., Al-Husaini, M., Bishop, J.M., Burt, J.A., Choat, J.H., Collette, B.B., Feary, D.A., Hartmann, S.A., Iwatsuki, Y., Kaymaram, F., Larson, H.K., Matsuura, K., Motomura, H., Munroe, T., Russell, B., Smith-Vaniz, W., Williams, J., Carpenter, K. E., 2019. Regional extinction risks for marine bony fishes occurring in the Persian/Arabian Gulf. *Biol. Conserv.* 230, 10–19.
- Carmo, F.F., Kamino, L.H., Junior, R.T., Campos, I.C., Carmo, F.F., Silvino, G., Castro, K. J., Mauro, M.L., Rodrigues, N.U.A., Miranda, M.P., Pinto, C.E.F., 2017. Fundão tailings dam failures: the environment tragedy of the largest technological disaster of Brazilian mining in global context. *Perspect. Ecol. Conserv.* 15, 145–151.
- Carvalho, V.F., Assis, J., Serrão, E.A., Nunes, J.M., Anderson, A.B., Batista, M.B., Barufi, J.B., Silva, J., Pereira, S.M.B., Horta, P.A., 2020. Environmental drivers of rhodolith beds and epiphytes community along the South Western Atlantic coast. *Mar. Environ. Res.* 154, 104827.
- Casado, P.A., Araújo, R., Bárbara, I., Bermejo, R., Borja, Á., Díez, I., Fernández, C., Gorostiza, J.M., Guinda, X., Hernández, I., Juanes, J.A., Peña, V., Peteiro, C., Puente, A., Quintana, I., Tuya, F., Viejo, R.M., Altamirano, M., Gallardo, T., Martínez, B., 2019. Distributional shifts of canopy-forming seaweeds from the Atlantic coast of Southern Europe. *Biodiversity and Conservation*, 28. *Biodiversity and Conservation*, pp. 1151–1172.
- Castelao, R.M., Barth, J.A., 2006. Upwelling around Cabo Frio, Brazil: the importance of wind stress curl. *Geophys. Res. Lett.* 33.
- Donelson, J.M., Sunday, J.M., Figueira, W.F., Gaitán-Espitia, J.D., Hobday, A.J., Johnson, C.R., Leis, J.M., Ling, S.D., Marshall, D., Pandolfi, J.M., Pecl, G., Rodgers, G.G., Booth, D.J., Munday, P.L., 2019. Understanding interactions between plasticity, adaptation and range shifts in response to marine environmental change. *Phil. Trans. Biol. Sci.* 374, 20180186.
- Elith, J., Leathwick, J.R., Hastie, T., 2008. A working guide to boosted regression trees. *J. Anim. Ecol.* 77, 802–813.
- Escobar, H., 2019. Mystery oil spill threatens marine sanctuary in Brazil. *Science* 366, 672–672.
- Filbee-Dexter, K., Wernberg, T., Grace, S.P., Thormar, J., Fredriksen, S., Narvaez, C.N., Feehan, C.J., Norderhaug, K.M., 2020. Marine heatwaves and the collapse of marginal North Atlantic kelp forests. *Sci. Rep.* 10, 13388.
- Floeter, S.R., Rocha, L.A., Robertson, D.R., Joyeux, J.C., Smith-Vaniz, W.F., Wirtz, P., Edwards, A.J., Barreiros, J.P., Ferreira, C.E.L., Gasparini, J.L., Brito, A., Falcón, J.M., Bowen, B.W., Bernardi, G., 2008. Atlantic reef fish biogeography and evolution. *J. Biogeogr.* 35, 22–47.
- Gomes, L.E.d.O., Correa, L.B., Sá, F., Neto, R.R., Bernardino, A.F., 2017. The impacts of the Samarco mine tailing spill on the Rio Doce estuary, Eastern Brazil. *Mar. Pollut. Bull.* 120, 28–36.

- Graham, M.H., Kinlan, B.P., Druehl, L.D., Garske, L.E., Banks, S., 2007. Deep-water kelp refugia as potential hotspots of tropical marine diversity and productivity. *Proc. Natl. Acad. Sci. U. S. A* 104, 16576–16580.
- Holz, V.L., Bahia, R.G., Karez, C.S., Vieira, F.V., Moraes, F.C., Vale, N.F., Sudatti, D.B., Salgado, L.T., Moura, R.L., Amado-Filho, G.M., 2020. Structure of rhodolith beds and surrounding habitats at the Doce river shelf (Brazil). *Diversity* 12, 75.
- Horta, P., Amancio, E., Coimbra, C., Oliveira, E., 2001. Considerações sobre a distribuição e origem da flora de macroalgas marinhas brasileiras. *HOEHNEA* 28, 243–265.
- IBGE, 2013. Atlas nacional de comércio e serviços, 1 ed. Parceria entre Ministério do Desenvolvimento, Indústria e Comércio Exterior, Instituto Brasileiro de Geografia e Estatística - IBGE, Instituto de Pesquisa Econômica Aplicada - IPEA e Serviço Brasileiro de Apoio às Micro e Pequenas Empresas - SEBRAE, Brasília, DF, Brazil, p. 157.
- IUCN, 2012. IUCN Red List - Criteria: Version 3.1. Gland. IUCN, Switzerland and Cambridge, UK.
- IUCN, 2020. The IUCN Red List of Threatened Species. Version 2020-1. <https://www.iucnredlist.org>. Accessed on June, 9th, 2020.
- Joly, A.B., Oliveira Filho, E.C., 1967. Two Brazilian laminarians. *Inst. Pesq. Mar.* 4, 1–13.
- Krumbholz, K.A., Okamoto, D.K., Rassweiler, A., Novak, M., Bolton, J.J., Cavanaugh, K.C., et al., 2016. Global patterns of kelp forest change over the past half-century. *Proc. Natl. Acad. Sci. Unit. States Am.* 113, 13785–13790.
- Lutchminarayam, K., 2018. Modelling Distribution and Associated Environmental Preferences of South African Kelps and Their Close Relatives. University of Cape Town, p. 103.
- Magris, R.A., Giarrizzo, T., 2020. Mysterious oil spill in the Atlantic Ocean threatens marine biodiversity and local people in Brazil. *Mar. Pollut. Bull.* 153, 110961.
- Marins, B.V., Amado-Filho, G.M., Barbarino, E., Pereira-Filho, G.H., Longo, L.L., 2014. Seasonal changes in population structure of the tropical deep-water kelp *Laminaria abyssalis*. *Phycol. Res.* 62, 55–62.
- Marins, B.V., Amado-Filho, G.M., Barreto, M.B.B., Longo, L.L., 2012. Taxonomy of the southwestern Atlantic endemic kelp: *Laminaria abyssalis* and *Laminaria brasiliensis* (Phaeophyceae, Laminariales) are not different species. *Phycol. Res.* 60, 51–60.
- Morrison, T.H., Adger, N., Barnett, J., Brown, K., Possingham, H., Hughes, T., 2020. Advancing coral reef governance into the anthropocene. *One Earth* 2, 64–74.
- Moss, R.H., Edmonds, J.A., Hibbard, K.A., Manning, M.R., Rose, S.K., van Vuuren, D.P., Carter, T.R., Emori, S., Kainuma, M., Kram, T., Meehl, G.A., Mitchell, J.F.B., Nakicenovic, N., Riahi, K., Smith, S.J., Stouffer, R.J., Thomson, A.M., Weyant, J.P., Wilbanks, T.J., 2010. The next generation of scenarios for climate change research and assessment. *Nature* 463, 747–756.
- Neiva, J., Assis, J., Coelho, N.C., Fernandes, F., Pearson, G.A., Serrão, E.A., 2015. Genes left behind: climate change threatens cryptic genetic diversity in the canopy-forming seaweed *Bifurcaria bifurcata*. *PloS One* 10 e0131530–e0131530.
- Oliveira Filho, E., 1976. Deep Water Marine Algae From Espírito Santo State (Brazil)/ Algas Marinhas de Profundidade do Estado do Espírito Santo. *Boletim de Botânica da Universidade de São Paulo*, pp. 73–79.
- Oliveira Filho, E.C., 1978. O Ciclo de Vida de *Laminaria brasiliensis* (Phaeophyta) no Laboratório. *Boletim de Botânica* 6, 1–7.
- Palóczy, A., Brink, K.H., da Silveira, I.C.A., Arruda, W.Z., Martins, R.P., 2016. Pathways and mechanisms of offshore water intrusions on the Espírito Santo Basin shelf (18°S–22°S, Brazil). *J. Geophys. Res.: Oceans* 121, 5134–5163.
- Pauly, D., Zeller, D., 2016. Catch reconstructions reveal that global marine fisheries catches are higher than reported and declining. *Nat. Commun.* 7, 10244.
- Pecl, G.T., Araújo, M.B., Bell, J.D., Blanchard, J., Bonebrake, T.C., Chen, I.-C., Clark, T.D., Colwell, R.K., Danielsen, F., Evengård, B., Falconi, L., Ferrier, S., Frusher, S., Garcia, R.A., Griffis, R.B., Hobday, A.J., Janion-Scheepers, C., Jarzyna, M.A., Jennings, S., Lenoir, J., Linnetved, H.I., Martin, V.Y., McCormack, P.C., McDonald, J., Mitchell, N.J., Mustonen, T., Pandolfi, J.M., Pettorelli, N., Popova, E., Robinson, S.A., Scheffers, B.R., Shaw, J.D., Sorte, C.J.B., Strugnell, J.M., Sunday, J.M., Tuanmu, M.-N., Vergés, A., Villanueva, C., Wernberg, T., Wapstra, E., Williams, S.E., 2017. Biodiversity redistribution under climate change: impacts on ecosystems and human well-being. *Science* 355, eaai9214.
- Phillips, S.J., Dudík, M., 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* 31.
- Phillips, S.J., Dudík, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J., Ferrier, S., 2009. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecol. Appl.* 19, 181–197.
- Quege, N., 1988. *Laminaria* (Phaeophyta) No Brasil, Uma Perspectiva Económica. Depto. de Botânica da Univ. de S. Paulo, São Paulo, Brazil, p. 230, 230.
- Queiroz, H.M., Nóbrega, G.N., Ferreira, T.O., Almeida, L.S., Romero, T.B., Santaella, S.T., Bernardino, A.F., Otero, X.L., 2018. The Samarco mine tailing disaster: a possible time-bomb for heavy metals contamination? *Sci. Total Environ.* 637–638, 498–506.
- Remya, K., Ramachandran, A., Jayakumar, S., 2015. Predicting the current and future suitable habitat distribution of *Myristica dactyloides* Gaertn. using the MaxEnt model in the Eastern Ghats, India. *Ecol. Eng.* 82, 184–188.
- Rodrigues, M.A., Dos Santos, C.P., Young, A.J., Strbac, D., Hall, D.O., 2002. A smaller and impaired xanthophyll cycle makes the deep sea macroalgae *Laminaria abyssalis* (Phaeophyceae) highly sensitive to daylight when compared with shallow water *Laminaria digitata*. *J. Phycol.* 38, 939–947.
- Rogers-Bennett, L., Catton, C.A., 2019. Marine heat wave and multiple stressors tip bull kelp forest to sea urchin barrens. *Sci. Rep.* 9, 15050.
- Rothman, M.D., Mattio, L., Anderson, R.J., Bolton, J.J., 2017. A phylogeographic investigation of the kelp genus *Laminaria* (laminariales, phaeophyceae), with emphasis on the south Atlantic Ocean. *J. Phycol.* 53, 778–789.
- Segurado, P., Araújo, M.B., Kunin, W.E., 2006. Consequences of spatial autocorrelation for niche-based models. *J. Appl. Ecol.* 43, 433–444.
- Senay, S.D., Worner, S.P., Ikeda, T., 2013. Novel three-step pseudo-absence selection technique for improved species distribution modelling. *PloS One* 8 e71218–e71218.
- Silberfeld, T., Leigh, J.W., Verbruggen, H., Cruaud, C., de Reviers, B., Rousseau, F., 2010. A multi-locus time-calibrated phylogeny of the brown algae (Heterokonta, Ochrophyta, Phaeophyceae): investigating the evolutionary nature of the “brown algal crown radiation”. *Mol. Phylogen. Evol.* 56, 659–674.
- Smale, D.A., Wernberg, T., Oliver, E.C.J., Thomsen, M., Harvey, B.P., Straub, S.C., Burrows, M.T., Alexander, L.V., Benthuyzen, J.A., Donat, M.G., Feng, M., Hobday, A.J., Holbrook, N.J., Perkins-Kirkpatrick, S.E., Scannell, H.A., Sen Gupta, A., Payne, B.L., Moore, P.J., 2019. Marine heatwaves threaten global biodiversity and the provision of ecosystem services. *Nat. Clim. Change* 9, 306–312.
- Steffen, W., Persson, A., Deutsch, L., Zalasiewicz, J., Williams, M., Richardson, K., Crumley, C., Crutzen, P., Folke, C., Gordon, L., Molina, M., Ramanathan, V., Rockstrom, J., Scheffer, M., Schellnhuber, H.J., Uno, S., 2011. The anthropocene: from global change to planetary stewardship. *Ambio* 40, 739–761.
- Thomsen, M.S., Mondardini, L., Alestra, T., Gerrity, S., Tait, L., South, P.M., Lilley, S.A., Schiel, D.R., 2019. Local extinction of bull kelp (*durvillaea spp.*) due to a marine heatwave. *Front. Mar. Sci.* 6, 84.
- Tyberghein, L., Verbruggen, H., Pauly, K., Troupin, C., Mineur, F., De Clerck, O., 2012. Bio-ORACLE: a global environmental dataset for marine species distribution modelling. *Global Ecol. Biogeogr.* 21, 272–281.
- Vasconcellos, M., Gasalla, M.A., 2001. Fisheries catches and the carrying capacity of marine ecosystems in southern Brazil. *Fish. Res.* 50, 279–295.
- Vergés, A., McCosker, E., Mayer-Pinto, M., Coleman, M.A., Wernberg, T., Ainsworth, T., Steinberg, P.D., 2019. Tropicalisation of temperate reefs: implications for ecosystem functions and management actions. *Funct. Ecol.* 33, 1000–1013.
- Wernberg, T., Bennett, S., Babcock, R.C., de Bettignies, T., Cure, K., Depczynski, M., Dufoix, F., Fromont, J., Fulton, C.J., Hovey, R.K., Harvey, E.S., Holmes, T.H., Kendrick, G.A., Radford, B., Santana-Garcon, J., Saunders, B.J., Smale, D.A., Thomsen, M.S., Tuckett, C.A., Tuya, F., Vanderklift, M.A., Wilson, S., 2016. Climate-driven regime shift of a temperate marine ecosystem. *Science* 353, 169–172.
- Wernberg, T., Krumbholz, K., Filbee-Dexter, K., Pedersen, M.F., 2019. Chapter 3 - status and trends for the world's kelp forests. In: Sheppard, C. (Ed.), *World Seas: an Environmental Evaluation*, second ed. Academic Press, pp. 57–78.
- Wilson, K.L., Skinner, M.A., Lotze, H.K., 2019. Projected 21st-century distribution of canopy-forming seaweeds in the Northwest Atlantic with climate change. *Divers. Distrib.* 25, 582–602.
- Yoneshigue-Valentin, Y., 2012. The life cycle of *Laminaria abyssalis* (Laminariales, Phaeophyta). In: Thirteenth International Seaweed Symposium: Proceedings of the Thirteenth International Seaweed Symposium Held in Vancouver, Canada, August 13–18, 1989. Springer Science & Business Media, pp. 461–466.
- Zuljević, A., Peters, A.F., Nikolić, V., Antolić, B., Despalatović, M., Cvitković, I., Isajlović, I., Mihanović, H., Matijević, S., Shewring, D.M., Canese, S., Katsaros, C., Küpper, F.C., 2016. The Mediterranean deep-water kelp *Laminaria rodriguezii* is an endangered species in the Adriatic Sea. *Mar. Biol.* 163, 69.

Extended references

- Braga AC, Yoneshigue-Valentin Y Nitrogen and phosphorus uptake by the Brazilian kelp *Laminaria abyssalis* (Phaeophyta) in culture. Fifteenth International Seaweed Symposium. Springer Netherlands.
- Braga, A.C., Yoneshigue-Valentin, Y., 1994. Growth of *Laminaria abyssalis* (Phaeophyta) at different nitrate concentrations. *Phycologia* 33, 271–274.
- Cosson, J., Yoneshigue-Valentin, Y., Deslandes, E., Coat, G., Floc'h, J.-Y., 1995. Résultats préliminaires sur la composition en alginates de *Laminaria abyssalis* des côtes brésiliennes. *Acta Bot. Gall.* 142, 137–140.
- Costa, P.A.S., Mincarone, M.M., Braga, A.C., Martins, A.S., Lavrado, H.P., Haimovici, M., Falcão, A.P.C., 2015. Megafaunal communities along a depth gradient on the tropical Brazilian continental margin. *Mar. Biol.* 11, 1053–1064.
- Dieck, T.I., Oliveira, E.C., 1993. The section *Digitatae* of the genus *Laminaria* (Phaeophyta) in the northern and southern Atlantic: crossing experiments and temperature responses. *Mar. Biol.* 115, 151–160.
- GBIF.org, 2019. GBIF Occurrence Download. <https://doi.org/10.15468/dl.3tkjrb>. Accessed March, 08/2019.
- Joly, A.B., 1967. Two Brazilian laminarians. *Inst. Pesq. Mar.* 4, 1–13.
- Marins, B.V., Amado-Filho, G.M., Barbarino, E., Pereira-Filho, G.H., Longo, L.L., 2014. Seasonal changes in population structure of the tropical deep-water kelp *Laminaria abyssalis*. *Phycol. Res.* 62, 55–62.
- Marins, B.V., Amado-Filho, G.M., Barreto, M.B.B., Longo, L.L., 2012. Taxonomy of the southwestern Atlantic endemic kelp: *Laminaria abyssalis* and *Laminaria brasiliensis* (Phaeophyceae, Laminariales) are not different species. *Phycol. Res.* 60, 51–60.
- Oliveira Filho, E.C., 1978. O Ciclo de Vida de *Laminaria brasiliensis* (Phaeophyta) no Laboratório. *Boletim de Botânica* 6, 1–7.
- Quége, N., 1988. Laminaria (Phaeophyta) No Brasil, uma Perspectiva Económica. Depto. de Botânica da Univ. de S. Paulo, São Paulo, Brazil, p. 230, 230 pp.
- Rodrigues, M.A., Dos Santos, C.P., Yoneshigue-Valentin, Y., Strbac, D., Hall, D.O., 2000. Photosynthetic light-response curves and photoinhibition of the deep-water *Laminaria abyssalis* and the intertidal *Laminaria digitata* (phaeophyceae). *J. Phycol.* 36, 97–106.
- Rodrigues, M.A., Dos Santos, C.P., Young, A.J., Strbac, D., Hall, D.O., 2002. A smaller and impaired xanthophyll cycle makes the deep sea macroalgae *Laminaria abyssalis* (Phaeophyceae) highly sensitive to daylight when compared with shallow water *Laminaria digitata*. *J. Phycol.* 38, 939–947.

- Rodrigues, M.A., Yoneshigue-Valentin, Y., Dos Santos, C.P., 1993. A comparative analysis of wild and laboratory grown *Laminaria abyssalis* (Phaeophyta) using modulated fluorescence. *Hydrobiologia* 260, 463–469.
- Romanos, M., Andrade-Serpa, M., Mourão, P., Yoneshigue-Valentin, Y., Costa, S., Pereira, M., Miranda, M., Gonçalves, J., Wigg, M., 2002. A sulphated fucan from the *Laminaria abyssalis* inhibits the human T cell lymphotropic virus type 1-induced syncytium formation in HeLa cells. *Antiviral Chem. Chemother.* 13, 219–221.
- Santelices, B., 2007. The discovery of kelp beds in deep-water habitats of tropical regions. *Proc. Natl. Acad. Sci. Unit. States Am.* 104, 19163–19164.
- Santos, M.G.M., Lagrota, M.H.C., Miranda, M.M.F.S., Yoneshigue-Valentin, Y., Wigg, M. D., 1999. A Screening for the Antiviral Effect of Extracts from Brazilian Marine Algae against Acyclovir Resistant Herpes Simplex Virus Type 1. *Botanica Marina. Book 42.*
- Yoneshigue-Valentin, Y., 1989. The life cycle of *Laminaria abyssalis* (Laminariales, Phaeophyta). In: Proc Thirteenth International Seaweed Symposium: Proceedings of the Thirteenth International Seaweed Symposium Held in Vancouver, Canada, August 13–18. Springer Science & Business Media.