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Manuela Bernardes Batista

ASPECTOS BIOGEOGRÁFICOS E FILOGENÉTICOS DE MACROALGAS MARINHAS NO ATLÂNTICO SUDOESTE

Florianópolis
2018

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Tese submetido ao Programa de Pós-Graduação em Ecologia da Universidade Federal de Santa Catarina para a obtenção do título de Doutora em Ecologia.
Orientador: Prof. Dr. Paulo Antunes Horta Júnior

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Manuela Bernardes Batista

Aspectos biogeográficos e filogenéticos de macroalgas marinhas no
Atlântico Sudoeste

O presente trabalho em nível de doutorado foi avaliado e aprovado por banca examinadora composta pelos seguintes membros:

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Certificamos que esta é a **versão original e final** do trabalho de conclusão que foi julgado adequado para obtenção do título de doutor em Ecologia.

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Florianópolis, 02 de março de 2018

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“Nos oceanos não há nada inútil. Tudo é parte do que faz os oceanos funcionarem” (Sylvia Earle).

RESUMO

A área de ocorrência das espécies depende da sua ecologia e história evolutiva, que por sua vez, são determinadas por interações entre uma variedade de fatores bióticos e abióticos atuando em diferentes escalas. Estes fatores podem atuar impondo uma limitação eco/fisiológica sobre a capacidade das espécies de persistir em uma determinada área ou ambiente. No ambiente marinho, a temperatura das massas d'água está entre os fatores com maior influência na delimitação e distribuição das comunidades bentônicas, principalmente as macroalgas. No entanto, as respostas eco-fisiológicas destes organismos podem variar do maior ao menor nível taxonômico, dependendo da sua história eco-evolutiva. Desta forma, entender as características dos nichos que as espécies ocupam e os processos que promovem a dispersão das espécies podem gerar resultados capazes de contribuir com programas de monitoramento de espécies invasivas, políticas de conservação de nicho e mudanças climáticas. Sendo assim, no Capítulo 1, abordamos a taxonomia em um âmbito global e avaliamos a diversidade críptica das espécies de “alface do mar”, do gênero *Ulva*, grupo generalizado como oportunista. Utilizando ferramentas moleculares, sugerimos mudanças na classificação taxonômica das espécies identificadas como *Ulva fasciata* e *Ulva lactuca* na costa do Brasil, além de outras regiões. Vale destacar que este trabalho contribuiu com as primeiras sequencias (*rbc*L) do gênero para a costa do Brasil. A análise filogenética e haplotípica revelou a existência de táxons cosmopolitas, como era o esperado, bem como táxons restritos a determinadas condições biogeográficas, principalmente regidas pela temperatura. Além disso, ao avaliar a diversidade críptica deste grupo no Atlântico Sudoeste, detectamos a presença de uma espécie exótica (*Ulva ohnoi*), considerada oportunista e invasora em várias partes do mundo. Ainda neste contexto, a detecção de outras duas espécies exótica no Atlântico Sudoeste foi abordada no Capítulo 2. Este estudo relatou a primeira ocorrência de jangadas de *Macrocystis pyrifera* e *Durvillaea antarctica* na costa temperada-quente do Atlântico Sudoeste. Nossos resultados indicam que um evento meteo-oceanográfico extremo, caracterizado por um deslocamento para o norte de águas oceânicas sub-antárticas, conduzidas por um ciclone extratropical, pode explicar essas ocorrências incomuns. Além disso, o modelo de nicho (MAXENT) baseado na distribuição de ocorrência destas espécies e em características ambientais revelou que há disponibilidade de nicho na região. Os preditores que mais influenciaram os modelos foram temperatura, irradiância e nutrientes. Os resultados desta tese confirmam que os *drivers* macroecológicos podem influenciar a distribuição e adaptação de espécies com diferentes características ecológicas. Além disso, trabalhos biogeográficos e filogenéticos são de extrema importância na detecção de espécies invasoras ou exóticas e que estas mesmas espécies podem se valer de diferentes vetores de dispersão, podendo ser de forma natural ou por vias antropogênicas.

Palavras-chave: Macroalgas marinhas, Atlântico Sudoeste, dispersão, filogenia, biogeografia, nicho ecológico.

ABSTRACT

The species occurrence area depends on their ecology and evolutionary history, which in turn, are determined by interactions between a variety of biotic and abiotic factors acting at different scales. These factors can act by imposing ecophysiological limitations on a specie's ability to persist in a given area or environment. In the marine environment, water temperature is among the factors with the greatest influence on the delimitation and distribution of benthic communities, mainly macroalgae. However, the ecophysiological responses of these organisms may vary from highest to lowest taxonomic level, depending on their eco-evolutionary history. Thus, understanding the characteristics of the niches that species occupy and the processes that promote their dispersion can generate results that are capable of contributing to invasive species monitoring programs, niche conservation policies and climate change. Therefore, in Chapter 1, we approach taxonomy from a global scope and evaluate the cryptic diversity of species of "sea lettuce", from the genus *Ulva*, a group that is generalized as opportunists. Using molecular tools, we suggest changes in the taxonomic classification of the species identified as *Ulva fasciata* and *Ulva lactuca* on the Brazilian coast, in addition to other regions. It is worth mentioning that this study produced the first sequences (*rbc*L) for this genus off the coast of Brazil. The phylogenetic and haplotypic analysis revealed the existence of cosmopolitan taxa, as was expected, as well as taxa restricted to certain biogeographical conditions, mainly governed by temperature. In addition, in assessing the cryptic diversity of this group in the Southwest Atlantic, we detected the presence of a non-indigenous species (*Ulva ohnoi*), which is considered opportunistic and invasive in several parts of the world. Still within this context, the detection of two other non-indigenous species in the Southwest Atlantic was discussed in Chapter 2. This study reported the first occurrence of rafts of *Macrocystis pyrifera* and *Durvillaea antarctica* on the warm temperate coast of the Southwest Atlantic. Our results indicate that an extreme meteo-oceanographic event, characterized by a northward displacement of sub-Antarctic oceanic waters, led by an extratropical cyclone, may explain these unusual occurrences. In addition, the niche model (MAXENT) that is based on the distribution of these species and on environmental characteristics revealed that there is niche availability in the region. The predictors that most influenced the models were temperature, irradiance and nutrients. The results of this thesis confirm that macroecological drivers can influence the distribution and adaptation of species with different ecological characteristics. In addition, biogeographical and phylogenetic studies are extremely important for the detection of invasive or non-indigenous species, and these same species can use different dispersion vectors, whether they are natural or anthropogenic pathways.

Keywords: Macroalgae, South Atlantic, dispersion, phylogeny, biogeography, niche.

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INTRODUÇÃO GERAL

1.1 Biogeografia e Macroecologia

Processos naturais e antropogênicos que promovem a dispersão e os padrões de distribuição da diversidade vêm sendo uma das grandes preocupações dentro da Biologia da Conservação (WHITTAKER *et al.*, 2005; SPALDING, MARK D *et al.*, 2007; FREDSTON-HERMANN *et al.*, 2018). A criação, a posição e desenho de unidades de conservação marinhas demandam de informações acerca não só da composição específica de sua biodiversidade, mas também de informações biogeográficas, relativas à sua representatividade em escala local/regional/global, assim como sobre processos que podem alimentar ou comprometer sua resiliência, contribuindo ou dificultando o fluxo gênico (FREDSTON-HERMANN *et al.*, 2018). A área de ocorrência das espécies, seja ela alvo de conservação ou não, depende da sua ecologia e história evolutiva, e é determinada por interações entre uma variedade de fatores bióticos e abióticos que atuam em diferentes escalas (PEARSON e DAWSON, 2003; ELITH e LEATHWICK, 2009). Fatores abióticos (por exemplo, luz, temperatura e salinidade) (SOBERON e PETERSON, 2005) assim como as interações inter e intraespecíficas (competição, predação, herbivoria, entre outras) (CASTILLA *et al.*, 2004) podem atuar impondo uma limitação eco/fisiológica sobre a capacidade da espécie de persistir em uma determinada área ou ambiente. A interação deste conjunto de condições (bióticos e abióticos) é comumente definida como nicho ecológico (HUTCHINSON, 1957).

Se por um lado as alterações ecológicas podem dificultar a expansão de certas populações (BROWN e MAURER, 1989), por outro, estas transformações podem favorecer aquelas que apresentam a capacidade ecológica/evolutiva (ou eco-evolutiva, *sensu* (LALLENSACK, 2018)) para aproveitar as novas condições (SOBERON e PETERSON, 2005). Portanto, as características de nicho podem ser interpretadas também como fenômenos eco-evolutivos (VERBRUGGEN *et al.*, 2009a). Mesmo com toda essa estrutura conceitual que prevê a distribuição geográfica de uma espécie, tem sido difícil caracterizar a escala espacial sobre a dispersão efetiva, especialmente para algas marinhas (NORTON, 1992; ECKMAN, 1996; KINLAN e GAINES, 2003; GAYLORD *et al.*, 2006).

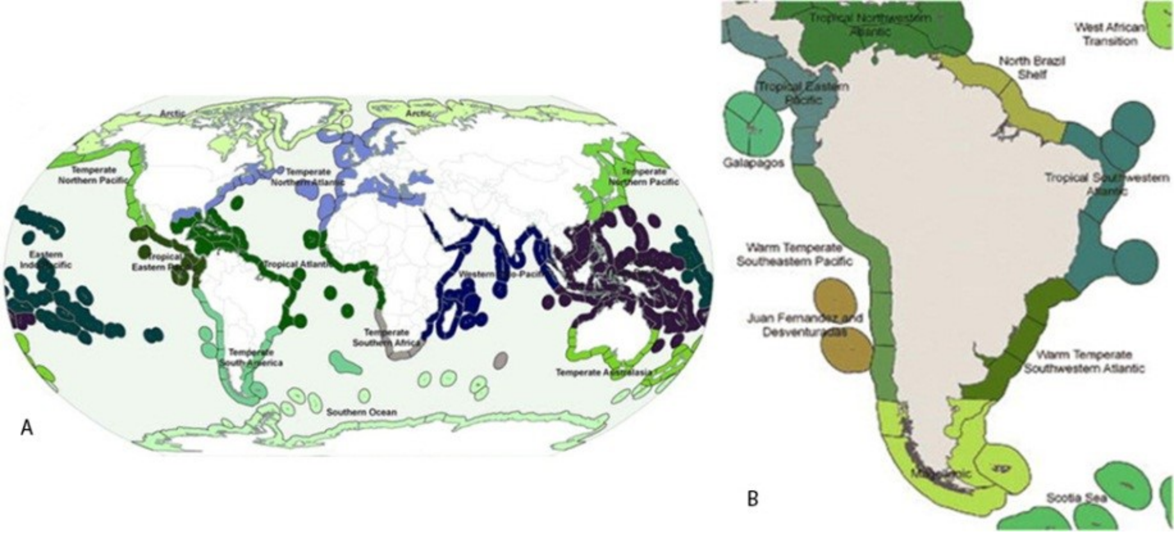
Espécies consideradas oportunistas, com maior plasticidade fenotípica, podem se valer de diferentes vetores para chegar em novas áreas, sejam estes naturais, crônicos ou agudos como os tsunamis que varreram a costa do Japão e promoveram dispersão transoceânica de um considerável número de espécies (THERRIAULT *et al.*, 2018). Por outro lado, espécies K estrategistas, que têm plasticidade fenotípica relativamente reduzida (SCHERNER *et al.*, 2012) apesar de poderem se beneficiar de vetores antropogênicos eventuais, desenvolveram mecanismos que promovem sua dispersão e mantêm a conectividade genética entre suas populações via processos naturais.

A natureza fluida do oceano pode aumentar a distância e o potencial de dispersão de muitos organismos marinhos. Embora os tipos de substrato variem espacialmente e os rios alterem os níveis locais de salinidade, um meio de dispersão único, contínuo (o oceano) conecta todo o habitat disponível. Logo, os gradientes ambientais dentro deste meio não são tão notáveis quanto em terra (GAYLORD e GAINES, 2000). Mesmo assim os limites de distribuição de muitas algas marinhas, invertebrados intertidal e subtidal e peixes costeiros agrupam-se em locais particulares (VALENTINE, 1966; VAN DEN HOEK, 1975; HAYDEN e DOLAN, 1976; HORN e ALLEN, 1978; MURRAY e LITTLER, 1981). Tais limites são frequentemente associados às descontinuidades oceanográficas e costeiras persistentes como: o ambiente térmico, em um contexto sazonal e o isolamento geográfico de determinada área costeira (SPALDING, MARK D *et al.*, 2007).

A temperatura das massas d'água como fator que limita a distribuição de recifes de corais e alguns bancos de algas é bem conhecida (*eg.*, (HUTCHINS, 1947; ABBOTT e NORTH, 1971; HAYDEN e DOLAN, 1976; SHAPIRO e HAUGEN, 1988; CLARKE, 1993), assim como não é novidade a sua aplicação em trabalhos de biogeografia (ADEY e STENECK, 2001). As macroalgas marinhas de forma geral, possuem uma ampla distribuição ecológica e geográfica, com algumas espécies sendo consideradas cosmopolitas. No entanto, outras muitas espécies de algas possuem tolerâncias térmicas marcadamente distintas, com ocorrências de populações limitadas à diferentes nichos climáticos (ASSIS *et al.*, 2017). Esta variabilidade macroecológica oferece modelos distintos, com estudos de caso para se buscar desvendar processos biogeográficos e evolutivos que determinam os padrões observados (VERBRUGGEN *et al.*, 2009a).

A classificação de províncias biogeográficas baseada na distribuição de organismos bentônicos, principalmente de algas, já é tradicionalmente aplicada em todo o mundo (VAN DEN HOEK, 1975; SPALDING, MARK D *et al.*, 2007; TUYA *et al.*, 2012). Na costa do Atlântico Sudoeste, são reconhecidas duas províncias biogeográficas principais: Tropical e Temperada Quente, além da região sub-antarctica (Fig.1) (SPALDING, MARK D. *et al.*, 2007). As regiões foram condicionadas pela variação extrema de pressões seletivas, tais como transparência da água, disponibilidade de substrato, extremos de temperatura, além da composição específica de organismos bentônicos que se limitam a zonas superficiais (fóticas) (HORTA *et al.*, 2001; SPALDING, MARK D *et al.*, 2007), onde os padrões de temperatura são mais complexos e melhor compreendidos (ADEY e STENECK, 2001).

Figura 1 – Mapas biogeográficos de áreas costeiras: A) Regiões biogeográficas marinhas do mundo. B) Províncias biogeográficas do Atlântico Sul.

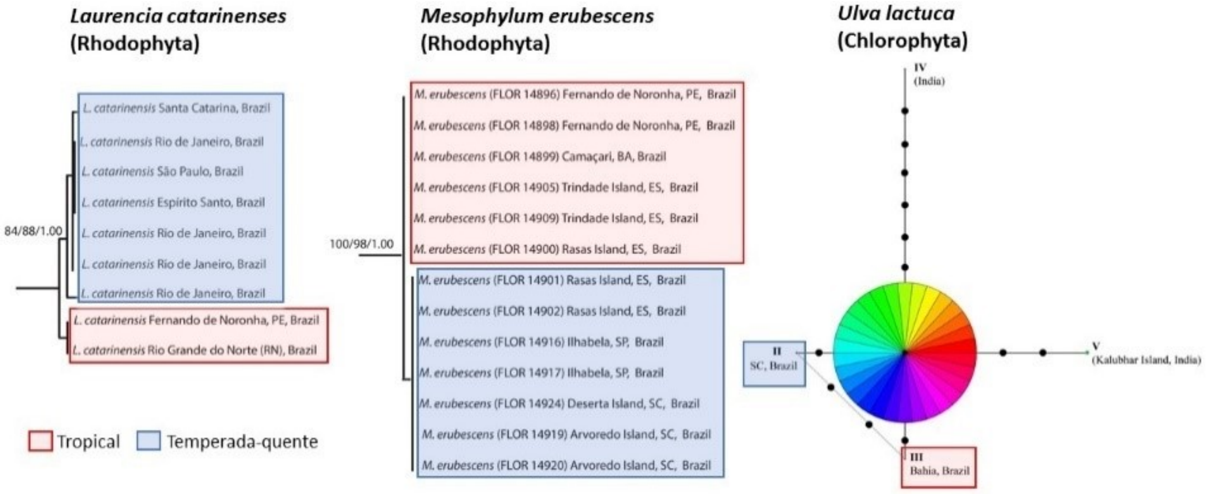


Fonte: Mapas retirados do trabalho de SPALDING et al., 2007.

Fluxos oceânicos em larga escala se originam em diferentes latitudes e profundidades e são compostos por massas de água com características distintas (MCGOWAN, 1971; POND e PICKARD, 1983; LONGHURST, 1995). As regiões biogeográficas no Atlântico Sudoeste estão sob a influência de diferentes correntes. A Corrente do Brasil, caracterizada por águas mais quentes e pobres em nutrientes, percorre a região ao largo da costa nordeste do país (Tropical) em direção ao sul (Temperado-quente). Aproximadamente entre as latitudes 36 ° e 39 ° S, estas águas tropicais confluem com as massas de água fria e sub-antarctica transportadas pela corrente das Malvinas (PETERSON e STRAMMA, 1991). Esta corrente atua como um ramo da Frente Sub-Antártica, que é o processo oceanográfico mais setentrional associado à Corrente Circumpolar Antártica na Passagem Drake (PETERSON e STRAMMA, 1991). O encontro dessas massas de águas frias com as águas tropicais da corrente do Brasil é conhecido como Convergência Subtropical. Nesta região, onde há grande produtividade biológica, é formada a água Central do Atlântico Sul (ACAS) (FREIRE *et al.,* 2017). Através de um sistema de correntes conhecido como Giro do Atlântico Subtropical, estas águas frias e ricas em nutrientes, ressurgem frequentemente durante o verão, em determinados pontos na costa do Brasil, como no Cabo do Farol de Santa Marta (SC) e Arraial do Cabo (RJ) (PEREIRA *et al.*, 2009).

Apesar da presença de uma multiplicidade de fatores que interagem e influencia a distribuição das espécies, características oceanográficas, como ecótones biogeográficas, podem afetar fortemente padrões de dispersão e alcance em espécies marinhas bentônicas com propágulos e larvas dispersantes (GAYLORD e GAINES, 2000; FOSSHEIM *et al.*, 2015). Este é um processo natural e já bem documentado, principalmente para peixes marinhos (ANDERSON *et al.*, 2017). Atualmente, alguns trabalhos abordando a biologia molecular de algas marinhas vem mostrando a presença de espécies com haplótipos restritos a determinadas regiões biogeográficas. Como é o caso da *Laurencia catarinenses* (Gouvêa et al. 2017), *Mesophylum erubescens* (Sissini et al., 2014b) e agora, *Ulva lactuca* (trabalho atual) que possuem diferenças moleculares marcantes entre as regiões Tropical e Temperada-quente da costa do Brasil (Fig. 2). No que diz respeito ao padrão de distribuição geográfica, este é resultante de uma complexa série de eventos histórico-evolutivos e ecológicos (Horta, 2000).

Figura 2 – Espécies que apresentaram divergência genética entre populações e nas diferentes regiões biogeográficas (Tropical e Temperada-quente) da costa brasileira. *L. catarinenses* (GOUVÊA et al., 2017); *M. erubescens* (SISSINI et al., 2014b); *U. lactuca* (neste trabalho).



Fonte: Modificado de GOUVÊA et al., 2017 e SISSINI et al., 2014b.

Algumas espécies de algas são conhecidas por sua capacidade de flutuar devido a presença de vesículas de ar ou de parênquimas aeríferos. Certas espécies de *Sargassum*, assim como alguns Kelps, como a gigante *Macrocystis pyrifera,* formam jangadas com capacidade de flutuar por longos períodos de tempo e por longas distâncias (MACAYA *et al.*, 2005; SISSINI *et al.*, 2016; BATISTA *et al.*, 2018). As alterações climáticas em andamento nos oceanos alteraram e devem aprofundar ainda mais as alterações na distribuição de massas d’água e potencialmente das rotas e alcance destes vetores de dispersão e conectividade genética marinha (CHEUNG *et al.*, 2013; FOSSHEIM *et al.*, 2015) com previsão de expandir-se nos limites de suas fronteiras (SUNDAY *et al.*, 2012).

Adicionalmente, para algumas espécies, atividades antrópicas como o transporte marítimo representa fonte de dispersão adicional (WONHAM e PACHEPSKY, 2006; LAPOINTE e BEDFORD, 2010; XU *et al.*, 2012; ANDERSON *et al.*, 2017). A translocação regional assistida por humanos tem contribuído com o registro de espécies exóticas ou invasoras em todo o mundo (BUCHAN e PADILLA, 1999; RUIZ e CARLTON, 2003; JOHNSON *et al.*, 2017). Neste caso, as algas marinhas estão entre os grupos mais comumente transportados através de vários vetores de transportes, como contaminação por incrustação em cascos de navios (JOHNSON *et al.*, 2017), água de lastro (FLAGELLA *et al.*, 2007; FLAGELLA *et al.*,

2010) e transporte na aquicultura e aquarismo (BOUDOURESQUE e VERLAQUE, 2002).

O registro de espécies de macroalgas não-nativas no Atlântico Sudoeste tem se tornado frequente nos últimos anos (AZEVEDO, CASSANO, JÚNIOR, BATISTA e OLIVEIRA, 2015; SISSINI *et al.*, 2016; BATISTA *et al.*, 2018). AZEVEDO *et al.*, 2015, registrou em 2011 na costa sul do Brasil a ocorrência de *Grateloupia turuturu Yamada*, uma espécie nativa do Pacífico, considerada a quinta espécie mais invasora entre as algas marinhas (NYBERG e WALLENTINUS, 2005). Os autores consideraram que a incrustação de cascos de embarcações seria o vetor mais provável para esta espécie. Recentemente, BATISTA *et al.,* 2018, detectou a chegada de “rafts” de espécies formadoras de Kelps, provindas da região subantártica, na costa do Uruguai e sul do Brasil. Nesta ocasião os autores relacionaram a dispersão destas massas flutuantes a eventos climáticos extremos, como a formação de um forte ciclone extratropical que ocorreu em setembro de 2016 no Atlântico Sudoeste. Outro registro foi a ocorrência de biomassa incomum de *Sargassum* flutuante na borda norte do Atlântico Sul (SISSINI *et al.*, 2016). Essa grande massa de algas flutuantes, foi observada no Arquipélogo de Fernando de Noronha, que é uma unidade de conservação de proteção integral (Parque Nacional Marinho de Fernando de Noronha). Este fenômeno foi relacionado a uma combinação de fatores que envolvem mudanças nos padrões de correntes, nas condições físico-químicas da água do mar e interações biológicas (SISSINI *et al.*, 2016).

Contudo, morfologia simples, plasticidade morfológica e diversidade críptica de muitas espécies de algas podem dificultar a sua identificação, muitas vezes passando despercebidas. Somados a isso, e à falta de informação sobre a distribuição natural de muitas espécies de algas, ficólogos, ecólogos e biólogos marinhos têm encontrado dificuldades para compreender e diagnosticar tais processos de invasão (MELTON *et al.*, 2016). Este é o caso das espécies do gênero *Ulva*, que são frequentemente membros conspícuos e localmente predominantes em uma variedade de habitats em todo o mundo. Devido a incongruências morfológicas relacionadas à grande plasticidade fenotípica, a real diversidade do gênero pode estar sendo mal interpretada (HAYDEN *et al.*, 2003). Desta forma, estudos moleculares vêm revolucionando a taxonomia do gênero (HAYDEN *et al.*, 2003), permitindo a identificação precisa e o rastreamento de espécies nocivas como aquelas formadoras de “marés verdes” (HIRAOKA *et al.*, 2004; LELIAERT *et al.*, 2009; MELTON *et al.*, 2016), além de fornecer um método objetivo para avaliar a real diversidade taxonômica deste gênero (O’KELLY *et al.*, 2010).

Apesar dos avanços, grande parte dos estudos moleculares realizados com espécies e populações de *Ulva*, se concentra em regiões temperadas ou boreais em mares da Europa (LOUGHNANE *et al.*, 2008), Nova Zelândia (HEESCH, 2007; HEESCH *et al.*, 2009), Austrália (KRAFT *et al.*, 2010; KIRKENDALE *et al.*, 2013), Japão (SHIMADA *et al.*, 2003; HIRAOKA *et al.*, 2004; SHIMADA *et al.*, 2008), China (DUAN *et al.*, 2012; KANG *et al.*, 2014), Península Ibérica (COUCEIRO *et al.*, 2011) oeste da América do Norte (HAYDEN *et al.*, 2003; HAYDEN e WAALAND, 2004). Na costa americana do Atlântico existem poucos trabalhos (GUIDONE e THORNBER, 2013), sendo apenas o trabalho de MELTON *et al*., (2016) com amostras de *Ulva ohnoi* Hiraoka et Shimada, coletada em regiões mais quentes na costa da Florida. Outras exceções em regiões tropicais, estão nos trabalhos de O’KELLY *et al*., (2010) no Hawaii e de KAZI et al. (2016) na Índia. Quase nenhum dado molecular está disponível para as espécies de *Ulva* em outras regiões tropicais, incluindo o Atlântico Sul. Ainda assim, a maior parte das espécies tropicais de *Ulva* é conhecida apenas por sua morfologia, e foram atribuídos nomes que se baseiam em tipos temperados, do hemisfério norte, principalmente os europeus (O’KELLY *et al.*, 2010), com áreas de conectividade natural, limitadas ao Atlântico Sul. Ademais, estudos relacionados à distribuição geográfica de haplótipos de *Ulva* são escassos. Portanto, contribuições neste sentido são importantes para elucidar a diversidade genética das espécies em todo o mundo e compreender os intervalos distributivos de táxons nativos e introduzidos (HANYUDA *et al.*, 2016).

Desta forma, este trabalho teve como objetivo compreender processos que promovem a dispersão de espécies que apresentam estratégias ecológicas distintas. No primeiro capítulo, utilizando-se ferramentas moleculares contribuímos para o esclarecimento da diversidade de espécies de “alface do mar”, grupo generalizado como oportunista. No segundo capítulo, contribuímos com o entendimento de processos ecológicos e oceanográficos que podem atuar como vetores de dispersão, invasão e conectividade de duas espécies K estrategistas, formadoras de florestas submersas. Por fim, apresentamos um apanhado dos principais resultados e sobre suas implicações para um processo de manejo e conservação costeira.

1.2 Bases para o entendimento dos capítulos:

Os estudos biogeográficos tendem a ser baseada em dados de presença / ausência de espécies. Devido à importância da determinação das espécies para compreender os padrões biogeográficos, ferramentas como a análise molecular se tornam de extrema importância.

Neste trabalho, utilizamos sequencias de DNA para identificar as amostras de *Ulva* coletadas ao longo da costa do Brasil e na Ilha de Fernando de Noronha (ver Fig. 1 do Capítulo 1). As algas coletadas são comumente chamadas de “alfaces-do-mar” devido ao formato do talo laminar, variando de orbiculares a alongadas (Fig. 3).

Figura 3 – Amostras dos dois tipos morfológicos de *Ulva* laminar coletadas durante o trabalho, na Pr. da Barra da Lagoa, SC, Brasil.

Cada indivíduo foi coletado com o auxílio de uma espátula para manter o espécime íntegro e com o apressório. Os espécimes foram separados individualmente e encaminhados ao laboratório dentro de uma caixa de isopor, protegidas da luminosidade e do calor. Em seguida, uma amostra de 2cm da borda de cada indivíduo foram separadas e limpas para a retirada de contaminantes como epífitas e substrato. Cada fragmento foi então armazenado dentro de um saco “zip” preenchido com sílica gel e etiqueta com identificação (Tabela 1). Posteriormente, as amostras eram encaminhadas para o processo de extração e amplificação do DNA, como descrito na seção de Materiais e Métodos do Capítulo 1.

Tabela 1 – Vouchers e informações de coleta das sequencias das espécies de *Ulva* coletadas na costa do Brasil

Voucher ID	**Species**	**Collection Site**	**Date Collected**	**Ecoregion**	**y**	**x**
U10_PT_B	Ulva sp.	Pr. da Pituba, Bahia, Brazil	29.04.2014	Tropical	-13.009071	-38.461003
U11_PT_B	Ulva sp.	Pr. da Pituba, Bahia, Brazil	29.04.2014	Tropical	-13.009071	-38.461003
U12_PT_B	Ulva sp.	Pr. da Pituba, Bahia, Brazil	29.04.2014	Tropical	-13.009071	-38.461003
U13_PT_B	Ulva sp.	Pr. da Pituba, Bahia, Brazil	29.04.2014	Tropical	-13.009071	-38.461003
U14_PT_B	Ulva sp.	Pr. da Pituba, Bahia, Brazil	29.04.2014	Tropical	-13.009071	-38.461003
U15_PT_B	Ulva sp.	Pr. da Pituba, Bahia, Brazil	29.04.2014	Tropical	-13.009071	-38.461003
U16_PT_B	Ulva sp.	Pr. da Pituba, Bahia, Brazil	29.04.2014	Tropical	-13.009071	-38.461003
U17_PT_B	Ulva sp.	Pr. da Pituba, Bahia, Brazil	29.04.2014	Tropical	-13.009071	-38.461003
U18_PT_B	Ulva sp.	Pr. da Pituba, Bahia, Brazil	29.04.2014	Tropical	-13.009071	-38.461003
U19_PT_B	Ulva sp.	Pr. da Pituba, Bahia, Brazil	29.04.2014	Tropical	-13.009071	-38.461003
U2_PT_BA	Ulva sp.	Pr. da Pituba, Bahia, Brazil	29.04.2014	Tropical	-13.009071	-38.461003
U20_PT_B	Ulva sp.	Pr. da Pituba, Bahia, Brazil	29.04.2014	Tropical	-13.009071	-38.461003
U3_PT_BA	Ulva sp.	Pr. da Pituba, Bahia, Brazil	29.04.2014	Tropical	-13.009071	-38.461003
U4_PT_BA	Ulva sp.	Pr. da Pituba, Bahia, Brazil	29.04.2014	Tropical	-13.009071	-38.461003
U5_PT_BA	Ulva sp.	Pr. da Pituba, Bahia, Brazil	29.04.2014	Tropical	-13.009071	-38.461003
U6_PT_BA	Ulva sp.	Pr. da Pituba, Bahia, Brazil	29.04.2014	Tropical	-13.009071	-38.461003
U8_PT_BA	Ulva sp.	Pr. da Pituba, Bahia, Brazil	29.04.2014	Tropical	-13.009071	-38.461003
U1_Gua_P	Ulva sp.	Guaratuba, Paraná, Brazil	27.07.2015	Warm Temperate	-25.888854	-48.562521
U2_Gua_P	Ulva sp.	Guaratuba, Paraná, Brazil	27.07.2015	Warm Temperate	-25.888854	-48.562521
U3_GUA_P	Ulva sp.	Guaratuba, Paraná, Brazil	27.07.2015	Warm Temperate	-25.888854	-48.562521

U4_GUA_P	Ulva sp.	Guaratuba, Paraná, Brazil	27.07.2015	Warm Temperate	-25.888854	-48.562521
U7_FN_RN	Ulva sp.	Rio Grande do Norte, Brazil	01.04.2015	Tropical	-3.834537	-32.397992
U8_FN_RN	Ulva sp.	Rio Grande do Norte, Brazil	01.04.2015	Tropical	-3.83416	-32.397936
U1_FSM_SC	Ulva sp.	Farol de Santa Marta, Santa Catarina, Brazil	31.06.2014	Warm Temperate	-28.60025	-48.817443
U2_FSM_S	Ulva sp.	Farol de Santa Marta, Santa Catarina, Brazil	31.06.2014	Warm Temperate	-28.60025	-48.817443
U3_FSM_SC	Ulva sp.	Farol de Santa Marta, Santa Catarina, Brazil	31.06.2014	Warm Temperate	-28.60025	-48.817443
U6_FSM_SC	Ulva sp.	Farol de Santa Marta, Santa Catarina, Brazil	31.06.2014	Warm Temperate	-28.60025	-48.817443
U9_FSM_SC	Ulva sp.	Farol de Santa Marta, Santa Catarina, Brazil	31.06.2014	Warm Temperate	-28.60025	-48.817443
U15_FSM_	Ulva sp.	Farol de Santa Marta, Santa Catarina, Brazil	31.06.2014	Warm Temperate	-28.60025	-48.817443
UR_CLB_SC	Ulva sp.	Costa da Lagoa da Conceição, Santa Catarina, Brazil	01.11.2015	Warm Temperate	-27.576341	-48.422945
U10_BL_SC	Ulva sp.	Prainha da Barra da Lagoa, Florianópolis, Santa Catarina, Brazil	23.02.2016	Warm Temperate	-27.574189	-48.420744
U14_BL_SC	Ulva sp.	Prainha da Barra da Lagoa, Florianópolis, Santa Catarina, Brazil	23.02.2016	Warm Temperate	-27.574189	-48.420744
U15_BL_SC	Ulva sp.	Prainha da Barra da Lagoa, Florianópolis, Santa Catarina, Brazil	23.02.2016	Warm Temperate	-27.574189	-48.420744
U18_BL_SC	Ulva sp.	Prainha da Barra da Lagoa, Florianópolis, Santa Catarina, Brazil	23.02.2016	Warm Temperate	-27.574189	-48.420744
U2_BL_SC	Ulva sp.	Prainha da Barra da Lagoa, Florianópolis, Santa Catarina, Brazil	23.02.2016	Warm Temperate	-27.574189	-48.420744
U3_BL_SC	Ulva sp.	Prainha da Barra da Lagoa, Florianópolis, Santa Catarina, Brazil	23.02.2016	Warm Temperate	-27.574189	-48.420744
U4_BL_SC	Ulva sp.	Prainha da Barra da Lagoa, Florianópolis, Santa Catarina, Brazil	23.02.2016	Warm Temperate	-27.574189	-48.420744
U6_BL_SC	Ulva sp.	Prainha da Barra da Lagoa, Florianópolis, Santa Catarina, Brazil	23.02.2016	Warm Temperate	-27.574189	-48.420744
U8_BL_SC	Ulva sp.	Prainha da Barra da Lagoa, Florianópolis, Santa Catarina, Brazil	23.02.2016	Warm Temperate	-27.574189	-48.420744
U1_Taq_SC	Ulva sp.	Pr. de Taquarinhas, Balneário Camboriú, Santa Catarina, Brazil	02.12.2015	Warm Temperate	-26.99509	-48.582456
U16_Taq_	Ulva sp.	Pr. de Taquarinhas, Balneário Camboriú, Santa Catarina, Brazil	02.12.2015	Warm Temperate	-26.99509	-48.582456
U17_Taq_	Ulva sp.	Pr. de Taquarinhas, Balneário Camboriú, Santa Catarina, Brazil	02.12.2015	Warm Temperate	-26.99509	-48.582456
U3_Taq_SC	Ulva sp.	Pr. de Taquarinhas, Balneário Camboriú, Santa Catarina, Brazil	02.12.2015	Warm Temperate	-26.99509	-48.582456
U5_Taq_SC	Ulva sp.	Pr. de Taquarinhas, Balneário Camboriú, Santa Catarina, Brazil	02.12.2015	Warm Temperate	-26.99509	-48.582456
U6_Taq_SC	Ulva sp.	Pr. de Taquarinhas, Balneário Camboriú, Santa Catarina, Brazil	02.12.2015	Warm Temperate	-26.99509	-48.582456

U7_Taq_SC	Ulva sp.	Pr. de Taquarinhas, Balneário Camboriú, Santa Catarina, Brazil	02.12.2015	Warm Temperate	-26.99509	-48.582456
U9_Taq_SC	Ulva sp.	Pr. de Taquarinhas, Balneário Camboriú, Santa Catarina, Brazil	02.12.2015	Warm Temperate	-26.99509	-48.582456

A região do DNA escolhida para comparar as sequencias obtidas na costa do Brasil com as demais disponíveis no Genbank (Tabela A2), foi a subunidade grande de plastídio da rubisco (*rbc*L), presente no genoma do cloroplasto. Este marcador é considerado informativo e possui alta resolução filogenética para este grupo (SAUNDERS e KUCERA, 2010). Além disso, o *rbc*L tem sido empregado extensivamente para resolver problemas taxonômicos e filogenéticos em macroalgas marinhas verdes, especialmente para o gênero *Ulva* (*eg*., (HAYDEN *et al*., 2003; SHIMADA *et al*., 2003; HAYDEN e WAALAND, 2004; HEESCH, 2007; KIRKENDALE *et al*., 2013; KANG *et al*., 2014). Devido a disso, é o marcador com maior número de sequências de *Ulva* disponíveis no Genbank, o que o torna apropriado para a ampla avaliação realizada no Capítulo 1.

Assim, foi possível realizar uma comparação filogenética com sequências de algas em escala global. A partir dos resultados filogenéticos, optamos por verificar a diversidade genética da linhagem genealógica à qual as alfaces-do-mar da costa do Brasil pertencem. Analisamos sua distribuição e conectividade geográfica, através de análises filogeográficas. Para isso, utilizamos análises de rede de haplótipos e índices de diversidade genética. O mesmo foi realizado com os espécimes de *Ulva onhoi* M. Hiraoka & S. Shimada detectado pela primeira vez no Atlântico Sul. No entanto, a não formação de rede de haplótipos devido à baixa diversidade genética presente nos espécimes do clado, pode indicar que este é um táxon recentemente introduzido na região (ver discussão do Capítulo 1).

Durante a realização deste trabalho, foi detectado também a presença de outras duas espécies exóticas na costa sul do Brasil e Uruguai entre os meses de agosto e setembro de 2016. No Brasil, as espécies foram encontradas flutuando, e de forma arribada nas praias do Campeche, Ilha de Santa Catarina. Os indivíduos encontrados foram coletados e encaminhados ao Laboratório de Ficologia da Universidade Federal de Santa Catarina, onde foram identificadas ao menor nível taxonômico com base nos seus caracteres morfológicos (Capítulo 2).

As espécies identificadas foram *Durvillaea antarctica* (Chamisso) Hariot, pertencente a ordem Fucales e *Macrocystis pyrifera* (Linnaeus) C. Agardh a ordem Laminariales. Estas espécies são conhecidas por formar grandes florestas de algas marinhas pardas em ambientes frios e regiões temperadas. Devido à afinidade com climas temperados e a distância geográfica entre o local onde foram encontradas e os locais de provável origem, foram aplicados diversos métodos para entender quais os processos oceanográficos e ecológicos, podem ter possibilitado a dispersão destes organismos para outra região biogeográfica.

Alguns autores de estudos de biogeografia enfatizam que esta disciplina é uma ciência de áreas habitadas por organismos, mais que uma ciência dos próprios organismos (NELSON e PLATNICK, 1981). Após certificarmos que estas espécies chegaram à costa Temperada-quente do Brasil ainda vivas (ver M&Ms no Capítulo 2), foram realizados estudos das condições oceanográficas durante e nos meses anteriores ao evento de dispersão. A caracterização oceanográfica foi baseada em dados de temperatura da superfície do mar (SST), bem como suas anomalias e a ocorrência de possíveis eventos climáticos extremos. Estas informações foram adquiridas na plataforma de dados disponíveis do NOAA para o Atlântico Sudoeste (https://coralreefwatch.noaa.gov/satellite/bleaching5km/index.php) e analisadas em parceria com o Instituto Oceanográfico da Universidade de São Paulo, através do PODAAC (Physical Oceanography Distributed Active Archive Center).

Outro fator importante seria avaliar a área disponível ou adequada para *D. antarctica* e *M. pyrifera* com base nas características ambientais e ocorrência pretéritas das espécies. Tal metodologia é extremamente útil para distinguir entre nicho fundamental e nicho potencial (VERBRUGGEN *et al.*, 2009a). Desta forma, optamos por utilizar ferramentas como o modelo macroecológico MaxEnt. Para isso, foi realizado uma extensa busca de registro georreferenciados tanto de *M. pyrifera* quanto de *D. antarctica*, obtidos através de revisão bibliográficas em artigos publicados e em bancos de dados como o GBIF (Global Biodiversity Information Facility). Com isso, gerou-se uma matriz de dados de ocorrência com um total de 889 registros para *M. pyrifera* e 616 para *D. antartica*. As variáveis ambientais usadas para gerar modelos de nicho foram baixadas do Bio-Oracle (TYBERGHEIN *et al.*, 2012b), para o oceano global. A seleção das variáveis foi baseada na biologia e na ecologia das espécies de “floresta” de algas (ASSIS *et al.*, 2017).

Por fim, nossos resultados permitiram afirmar que uma combinação de fortes ventos oriundos de ciclones extratropicais e mudanças na velocidade e SST de correntes costeiras, podem ter impulsionado estas jangadas até a costa do Brasil. Além disso, os resultados dos modelos de nicho indicam que a área disponível para adequação de nicho das espécies é extensamente maior que a área conhecida ocupada por elas. Estes resultados são amplamente discutidos no Capítulo 2.

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CAPÍTULO 1

UNTANGLING THE COMPLEX SEA LETTUCE SYSTEMATIC

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ABSTRACT

Among observed changes related to coastal pollution, the abundance and sometimes dominance of sea lettuce, green seaweeds represented by the genus Ulva L. deserve special attention. In many cases where these seaweed bloom, forming green tides, with economic and ecological impacts, the responsible species are invasive. Here we provide a molecular evaluation of *Ulva* systematic, considering main taxa circumscription and identification of cryptic species in Brazilian coast. Among the main 14 phylogeographical groups deserve special attention the segregation between *U. lactuca,* from temperate areas, and *U. fasciata* a cosmopolitan group. Considering cryptic species, in northeastern Brazilian coast was identified the *U. ohnoi,* a green tide formation species with invasion related to ballast water. Our result reinforces the importance of molecular characterization of Ulva genus, as a major source of information in the taxonomical infrageneric evaluation. Natural or even anthropogenic vectors should be monitored regarding bioinvasion avoidance and coastal management, with special attention to MPAs.

Keywords: *Ulva*, phylogeny*, Ulva ohnoi*, genetic diversity, biogeography

1.INTRODUCTION

Human population growth and urbanization of coastal areas produced environmental constraints at local (MARTINS *et al.*, 2012), regional (SCHERNER *et al.*, 2013) and global scales (HALPERN *et al.*, 2008). Among observed changes related with coastal pollution, the abundance and sometimes dominance of sea lettuce, green seaweeds represented by the genus *Ulva L*. deserve special attention. They are main constituents of benthic communities in many urbanized intertidal environments (SCHERNER *et al.*, 2012) and responsible by most green tides phenomena around the world (WANG *et al.*, 2015; VAN ALSTYNE, 2016). *Ulva* blooms are apparently related to eutrophication of the environment, specially caused by the interactions of resource availability (*e.g.,* nutrients originated from sewage, agricultures and aquaculture effluents), exclusion of competitors and predators, (*eg.,*(RAFFAELLI, 2000; HIRAOKA *et al.*, 2004)). These algae species ecological success is attributed to its capacity to use surplus nutrients (ANDREAKIS e SCHAFFELKE, 2012).

Ulva encompasses the richest genus within Ulvaceae family (HEESCH, 2007). Among its 400 species, 141 have a current taxonomic status; 155 are considered homotypic or heterotypic synonyms; others with uncertain taxonomic status (GUIRY e GUIRY, 2016). The taxonomic uncertainties present in the genus *Ulva* are related with the morphological plasticity (GAO *et al.*, 2016), and scarcity of diagnostic features, once the distromatic and foliose thallus are globally represented inducing taxonomic simplifications and misidentifications, once they often exhibit intraspecific variation and interspecific overlap (HOFMANN *et al.*, 2010). Such fragile framework, constituted by many cryptic species, preclude robust biogeographic interpretations, clear understanding of connectivity, dispersal processes, and subsequent production of key information to provide efficient coastal management, specially regarding green tides phenomena worldwide (PERROT *et al.*, 2014; KAZI *et al.*, 2016).

Due to its abundance and ecological importance, the genus received considerable attention regarding taxonomical efforts which have been relying on different morphological and anatomical aspects to provide refined species identification (KOEMAN e VAN DEN HOEK, 1981; TANNER, 1986). Such effort (baseline) resulted in cosmopolitan species, apparently found all over the world, in a wide range of habitats and environments (KOEMAN e VAN DEN HOEK, 1981). Some species can be easily found attached to rocky shallows on the upper portion of the tidal region, while others on subtidal habitats, up to 40 meters deep (CHAPMAN, 1956; ADAMS, 1994). Due to salinity variation tolerance, some species may grow under marine, estuarine and brackish conditions. In addition, they can be found both in environments strongly impacted by anthropic activities and in pristine environments, being referred as excellent bioindicators in response to eutrophication of the coastal zone (KOZHENKOVA *et al.*, 2006). *Ulva* species ability to tolerate different environmental conditions, such as, severe light deprivation for up to 10 months (SANTELICES *et al.*, 2002), make them excellent dispersers. These species are among the most notorious organisms attached to ship hulls and ballast water (FLAGELLA *et al.*, 2010). In addition, some species exhibit invasive traits, such as high growth rates, efficient reproductive alternatives (LIU *et al.*, 2015).

Due to ecological and economic impacts generated by *Ulva* blooms, the characterization of these opportunistic species distributions, and detection of eventual non-native species with harmful potential, has become crucial to define management alternativies for coastal regions (WANG e WU, 2009). Recently, MELTON *et al*., (2016) identified *Ulva ohnoi* M. Hiraoka and S. Shimada as a new record for the Western Atlantic utilizing molecular tools. This invasive species is the main responsible green tides observed last years in Biscayne Bay, Florida. Relying on such robust identification, the authors reinforced that such species have high capacity to bloom, and the necessity for efficient management of such invasion process.

In this context, molecular tools have been an important ally, not only by tracking potentially harmful "green tide" species, but also, as an objective method to evaluate the taxonomy and cryptic diversity of the genus (KAZI *et al.*, 2016). To date, few molecular studies have been conducted on DNA sequences of the type species. In the case of *Ulva lactuca* L, which is also the holotype of the genus, the molecular identity of the type does not match the specimens attributed to this name (BUTLER, 2007). However, in a short review utilizing Google Scholar (www.scholar.google.com), and the key words "*Ulva lactuca*" and taxonomy, this taxon appears in 4,710 articles. Recently, a molecular study based on *rbc*L and ITS sequences, conducted in Hawaiian Islands, showed that specimens morphologically identified in the region as *Ulva fasciata* are actually synonym of *U. lactuca* (O'KELLY *et al.*, 2010). *Ulva fasciata* have been associated by scientists to warm temperate and tropical regions (PHILLIPS, 1988), molecular studies, otherwise, state that its occurrence is more limited than expected (HEESCH, 2007).

Most molecular studies conducted with *Ulva* species and populations are restricted to temperate and boreal waters of Europe (LOUGHNANE *et al.*, 2008), Northwestern America coast (HAYDEN e WAALAND, 2004; HOFMANN *et al.*, 2010), New Zealand (HEESCH, 2007; HEESCH *et al.*, 2009), Japan (SHIMADA *et al.*, 2003; HIRAOKA *et al.*, 2004; SHIMADA *et al.*, 2008), China (DUAN *et al.*, 2012; KANG *et al.*, 2014). Despite efforts accomplished in Hawaiian Islands (O'KELLY *et al.*, 2010) and in the west coast of India (KAZI *et al.*, 2016), there is still need for *Ulva* molecular information regarding tropical regions (O'KELLY *et al.*, 2010). The identifications of *Ulva* tropical species are given only by morphological analysis, with attributed names of the type species described in temperate regions, mainly European ones (O'KELLY *et al.*, 2010).

Southwestern Atlantic Ocean, specifically the Brazilian coast, there is a lack of molecular studies for genus *Ulva*. Its species are among the most conspicuous and dominant species of benthic environments in the region, especially in urbanized areas (SCHERNER *et al.*, 2013). Considering the global process of dispersion, invasion, and connectivity, Brazilian coast can hold fundamental information to untangle its systematic and complete the puzzle of these enigmatic sea lettuces. This study is the first molecular approach, based on data from *rbc*L, of *Ulva* species with foliose morphology and distromatic anatomy for the Brazilian coast. Here we analysed 277 chloroplast-encoded gene sequences (43 from this study), we revisited the genus systematic and proposed the segregation of *Ulva lactuca* and *U. fasciata*. Complementing the marine knowledge of south Atlantic marine flora, we detect the presence of *U. ohnoi*, a possible non-native species occurring in Brazilian MPAs.

2. MATERIALS AND METHODS

2.1 Study area

The Brazilian coast extends almost 9500 km, with environments changing from tropical (lower lattitudes) to warm temperate (higher latitudes) (HORTA *et al.*, 2001). The occurrence of reefs is widespread along the coast occurring at least on a third of the coastline, with biogenic reefs predominating in the north (0°52′N-19°S) and rocky reefs in the south (20°-28°) (FLOETER *et al.*, 2006). Considering Brazilian coastal ecoregions seawater temperature increases towards the north with average surface temperatures of 24°C (from Rio Grande do Sul State to São Paulo Sate), in the southeast region, 24°C in the transitional zone (Espírito Santo State), and 28°C from E. Santo to the coast of Pernambuco (Fig. 1). The coast of Espírito Santo is influenced by low temperature, nutrient-rich water derived from an upwelling zone.

Most of seventeen Brazilian coastal states have their capitals near the coast. Even when the capital is not located on the coast, large cities have grown, such as the Baixada Santista metropolitan area, on the coast of São Paulo with a population of 1.7 million. In Espírito Santo the coastal urban sprawl around Vitória also has 1.9 million people whereas in the north-eastern state of Pernambuco, Recife and neighbouring cities have 3.7 million people (IBGE, 2010). In addition, there are medium sized coastal cities with relatively high numbers of dwellings, which increase in population density due to tourism in the holidays and summer months.

The Archipelago of Fernando de Noronha, (3°54`S - 32°25`W), lies 360 km offshore and comprises 21 islands, covering 26 km^2. Average seawater surface temperature ranges from 26 to 28°C yearly. The archipelago has 3500 resident all concentrated on the main island. Since 1988 2/3 of its terrestrial territory has been protected as a National Park and the remaining territory is populated with restrictions, as an Environmental Protection Area. Thus, urbanization on the archipelago is very low, especially along the coast. Three areas were surveyed in the archipelago: Caieira, Praia do Porto and Praia do Leão. Caieira faces east and Praia do Leão faces southeast. Praia do Porto is located in the Santo Antonio Bay, facing northwest, and has daily boat traffic.

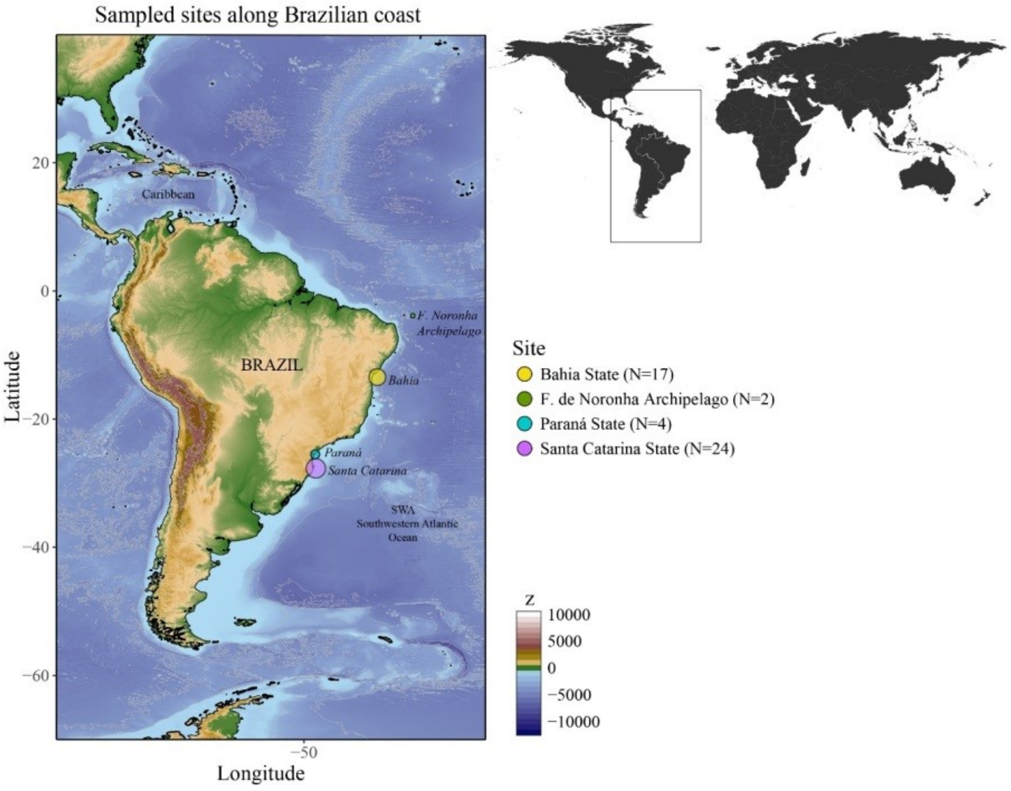
2.2 Species sampling and DNA sampling

Collectors focused on sampling individuals with a distinct sea lettuce morphotype: elongated leaves. Such morphology is generally applied in traditional taxonomic identification for species, such as *Ulva lactuca*, *Ulva fasciata* and *Ulva* rigida (TAYLOR, 1931). Species with cylindrict morphology were not sampled. Samples were collected at 6 points between latitudes 13° 00’32.64” S; 38°27’39.61” W and 28°36’00.82” S; 48°49’01.95” W on the Brazilian coast (Fig. 1). Twenty individuals were randomly collected from the tidal region of each sampled locality. In

Fernando de Noronha Archipelago, Pernambuco State, Brazil (3°50’50.70” S; 32°26’02.51” W), just two specimens of *Ulva* sp. were identified and collected. Samples were placed in individual plastic bags and transported to the laboratory in a refrigerated container, then qualified and tagged with a specific coded serial number (*e.g., Ulva* sp, number, beach, state) (Table A2).

For molecular studies, a 2 x 2 cm fragment of the largest leave of each individual were removed and inserted in small paper bags to avoid crumbling, subsequently, samples were sealed in zip-lock plastic bags, filled by dry silica gel. Such tissue quantity characterized sufficient material for more than one DNA extraction. Plastic bags were then stored in The Phycology Laboratory, Federal University of Santa Catarina, and kept away from light and excessive heat exposure. One example of each sample was fixed in 4% formoldehyde diluted in sea water, for posterior morphological observations. All the vouchers of the collected material are currently retained in the Laboratory of Phycology of the Federal University of Santa Catarina and will ultimately be deposited in the FLOR Herbarium.

Figure 4 – Sampled sites along the Brazilian coast and number of DNA sequences used in the study.



2.3 Molecular studies

2.3.1 DNA extraction and amplification

Species identifications were based on DNA sequence data combination and morphological knowledge. About 10 mg of dried *Ulva* tissue were used for DNA extraction from samples obtained in Brazilian coast. Samples were placed in a 1.5 ml Eppendorf tube, frozen with liquid nitrogen and ground for 2 minutes with a plastic pestle. DNA was extracted using a commercial kit [NucleoSpin® Plant II, Macherey-Nagel, Düren, Germany] followed the manufacturer's instructions. The large subunit of the plastid-encoded Ribulose Bisphosphate Carboxylase-Oxigenase (RuBisCO) gene region (*rbc*L) was amplified in a polymerase chain reaction (PCR), using the PCR master mix (Promega) following the manufacturer’s instructions. We used published primers pair RH1 and 1385r (MANHART, 1994) and cycling conditions described in LOUGHNANE *et al*. (2008). After amplification, we performed the purification of the PCR products using PEG 8000 (Polyethyleneglycol 8000) (LIS e SCHLEIF, 1975). Then, the PCR product was further quantified by visual estimation with 0.8% GelRed stained agarose gel (Biotium®) compared to the standard 1 kb band DNA scale (New England Biolabs®).

2.3.2 Sequencing

The purified PCR products were subsequently sequenced by the chain termination method (SANGER *et al.*, 1977), with the Big Dye Terminator v 3.1 kit (Thermo Scientific, Carlsbad, CA, USA) following the protocol specified by the supplier. Resulting cycle sequence reaction were purified with ETOH/EDTA precipitation and were either sequenced at Universidade Federal de Santa Catarina, Laboratório de Fisiologia do Desenvolvimento e Genética Vegetal on a 3500 XL - Applied Biosystems (Thermo Scientific) or at the ABI 3730 - Applied Biosystems. Resulting chromatograms were assembled using software Sequencing Analysis v6.0 (Thermo Scientific).

2.3.3 Alignments

Consensus sequences of *rbc*L regions were assembled from forward and reverse readings. We generated 47 new *rbc*L sequences (1141 bp) (Table A2). Quality analysis and editing of the consensus sequences were performed in Geneious version R9 (http: //www.geneious.com, Kearse et al., 2012). Concensus DNA sequences were aligned using Muscle method in MEGA 7.0.26 software

(Tamura et al., 2011). Other 215 *rbc*L sequences of the genus Ulva were downloaded from Genbank (Benson et al., 2004), and added to the alignment, including 2 sequences (*Umbraulva japonica* and *Umbraulva olivascens*) as outgroups. Sequences of locality type Ulva genus are not available on Genbank at this time. However, to other Genbank sequences of the *rbc*L gene inclusion in the alignment, certain criteria have been adopted which included: (i) having a minimum number of 1400 base pairs; (ii) all sequences of species with leaf stems were used; (iii) at least one representative of the other morphological types of the genus were used. For more information about the specimens from Genbank used in the matrix (please, see Table A2).

2.3.4 Phylogenetic analysis

The analyzes were conducted using Maximum Likelihood (ML) and Bayesian (MCMC) methods, both with a GTR+G model (REF). The ML analyses were performed using the with the RxML-HPC2 program using the online server 'The CIPRES Science Gateway V.3.3' (MILLER *et al.*, 2010) with 1000 replicates were run. Supporting for resulting relationships was estimated by 1000 bootstrap replicates. A Bayesian analyze was estimated using the MrBayes (RONQUIST e HUELSENBECK, 2003) plug-in, the following settings: 1,000,000 MCMC chain length, subsampling frequency 1,000, burn-in length 50,000, 4 heated chains, and temperature 0.2. A haplotype network was created using "pegas" Package R to illustrate the lineages spatial distributions (PARADIS, 2010). Haplotypic diversity (h) and nucleotid diversity (π) were calculated using foram calculadas em Arlequin 3.5 Haplotype networks based on the pasimony of each marquer were calculated and constructed in R using the "haploNet" function, "pegas" package 0,5-1. Haplotype frequences used were calculated in Arlequim software.

3 RESULTS

3.1 Molecular data and phylogenetic analyses

A total of 263 *rbc*L DNA sequences with 1141bp were used in this study, including 47 sequenced samples (Table A2). Of these, we must highlight the clades that segregate the taxa *U. rotundata, U. lobata, U. lactuca* (stricto sensu), *U. australis*, *U. linza*, *U. tanneri*, *U. californica*, *U. rigida*, *U. ohnoi*, and a last and well represented group characterized by a complex *U. lactuca/fasciata* complex. The 44

DNA sequence from Brazil remained in a monophyletic clade with other 54 GenBank samples, in the phylogenetic analyzes MCMC (Fig. 2) and ML. (Fig. A1). This clade was cut from MCMC analysis where it is possible to observe that the largest sequences number are identified as *Ulva lactuca*, followed of *U. fasciata*, and also *Ulva reticulata* Forsskål*, Ulva rigida* C. Agardh*, Ulva scandinavica* Bliding *and Ulva rotundata* Bliding (Fig.3). This is also the more frequently characterized clade (ML and MCMC).

Only 1 sequence (U1_FSM_SC) from southern Brazil did not coincide with any GenBank sequence. Other two sequences samples from Fernando de Noronha were identical to previously published *Ulva ohnoi* M. Hiraoka & S. Shimada sequences from Japan (seven sequences; HIRAOKA *et al.,* 2004), Hawaiian Islands (six sequences; O'KELLY *et al*., India (eight sequences; KAZI *et al*., 2016), USA (five sequences; MELTON *et al*., 2016). This included the *rbc*L sequence of the type specimen from Japan (AB116040).

An alignment with 99 *rbc*L sequences was generated from Brazilian samples which were grouped in the same clade with samples from Portugal (one sequence), Japan (three sequences; *Shimada et al*., 2003), New Zealand (two sequences; HEESCH *et al*., 2007), Hawaiian Islands (27 sequences, O'KELLY *et al*., 2010), USA (one sequence; MELTON & LOPEZ-BAUTISTA, 2015), United Kingdom (one sequence; LOUGHNANE *et al*.,2008), Ireland (two sequences, LOUGHNANE *et al*.,2008), Australia (two sequences, KRAFT *et al*., 2010), India (16 sequences), North Korea (one sequence; KANG *et al.,* 2014). This alignment was used for phylogenetic inference (Fig. 2) and to generate the haplotype network (Fig. 4).

The haplotype network presented 5 haplotypes (Fig. 4). Three haplotypes were present on the coast of Brazil: haplotype I, which is also present in all other regions; the haplotype II is restricted to tropical zone Haplotypes II and III, restricted to the warm-temperate zone. Haplotypes II and III only varied by a single base pair from haplotype 1, while haplotype II and III differed by two base pairs from each other. India had the highest number of differentiated haplotypes (Fig 4) and the highest index of genetic diversity (please verify values of Pi, Table 2).

Figure 2 – MCMC Bayesian tree run with 1.000.000 generations bootstraps basedon 1141 pb of the chloroplast- encoded *rbcL* molecular marker.

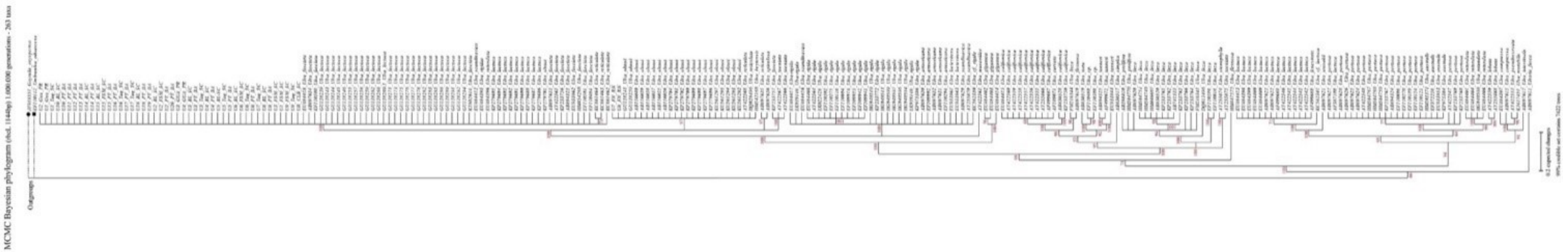


Figure 3 – Detail of the *Ulva lactuca* clade from the phylogram with samples of the Brazil badesed on MCMC Baysian (rbcL 1141pb) 1.000.000 generations - 262 samples. 99% credible set contains 7422 trees.

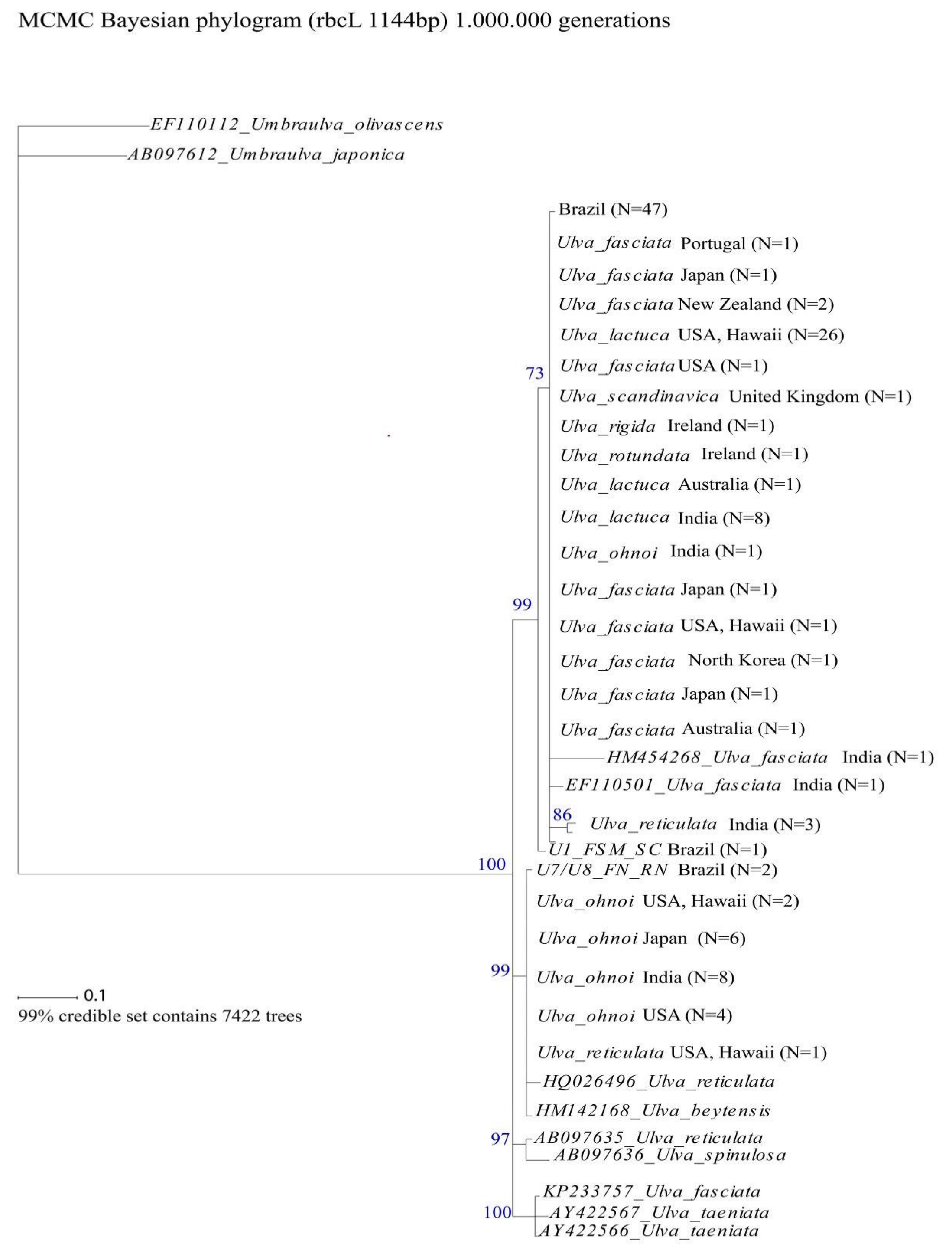


Figure 4 – The Median-joining haplotype network of 99 sequences of rbcL (1141bp) from *Ulva lactuca* samples from Brazil (45 sequences), Portugal (one sequences), Japan (tree sequences), New Zealand; USA (one sequence), United Kingdom (one sequence); Ireland (two se sequences), Australia (two sequences), India (14 sequences), North Korea (one sequence). The numbers in parentheses represent a scale of the number of sequences for each haplotype and black balls represents one change in a base pair.

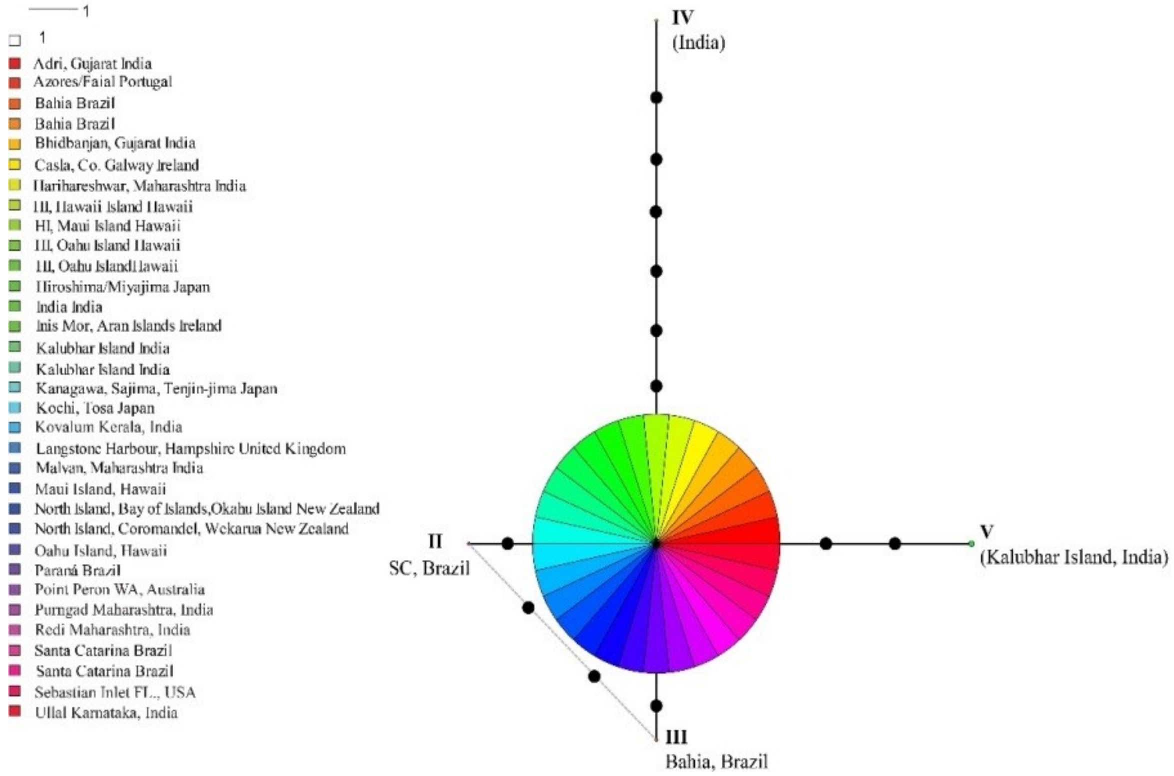


Table 1 – Haplotype frequencies in populations of *Ulva fasciata/lactuca* complex

Haplotype	**BR_SC**	**BR_BA**	**BR_PR**	**USA**	**IN**	**HW**	**PT**	**JP**	**N.Z**	**U.K**	**IR**	**AT**	**N. K**
	(24)	**(17)**	**(4)**	**(1)**	**(16)**	**(27)**	**(1)**	**(3)**	**(3)**	**(1)**	**(2)**	**(2)**	**(1)**
Hap_1	0.917	0.941	1	1	0.812	1	1	3	3	1	2	1	1
Hap_3	0	0.0588	0	0	0	0	0	0	0	0	0	0	0
Hap_2	0.0417	0	0	0	0	0	0	0	0	0	0	0	0
Hap_5	0	0	0	0	0.125	0	0	0	0	0	0	0	0
Hap_4	0	0	0	0	0.063	0	0	0	0	0	0	0	0

Table2 – Molecular diversity indexes

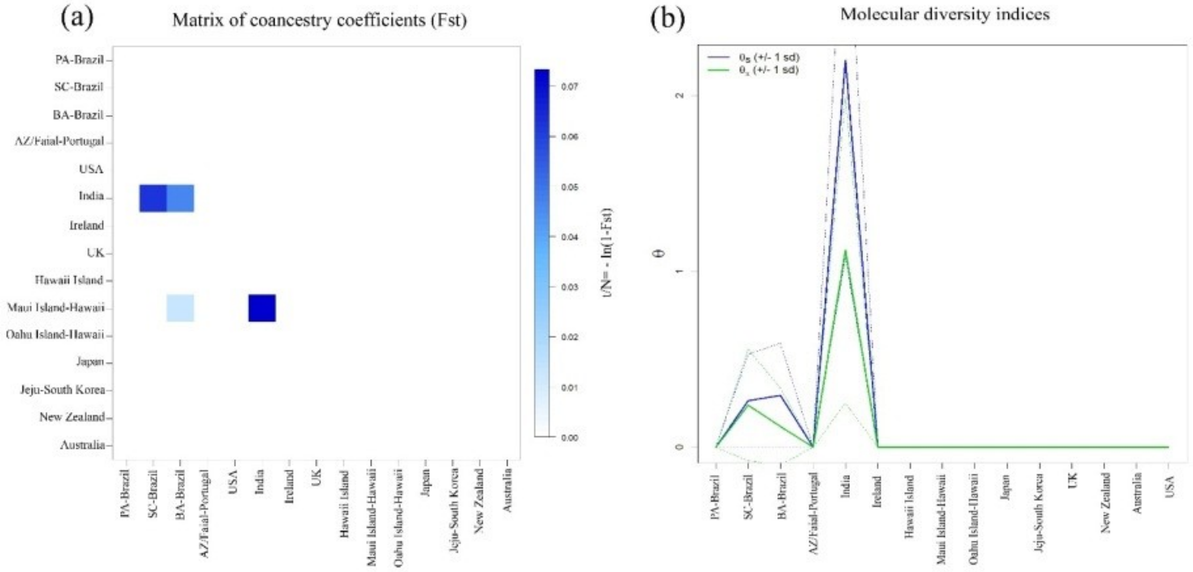
Statistics	**BR_SC**	**BR_BA**	**BR_PR**	**USA**	**IN**	**HW**	**PT**	**JP**	**N.Z**	**U.K**	**IR**	**AT**	**N. K**	**Mean**	**s.d**
N° of transitions	1	1	0	0	4	0	0	0	0	0	0	0	0	0.462	1.127
N°of transversions	0	0	0	0	3	0	0	0	0	0	0	0	0	0.231	0.832
N° of s substitutions	1	1	0	0	7	0	0	0	0	0	0	0	0	0.692	1.932
N° of indels	1	0	0	0	0	0	0	0	0	0	0	0	0	0.077	0.277
N° of ts. sites	1	1	0	0	4	0	0	0	0	0	0	0	0	0.462	1.127
N° of tv. Sites	0	0	0	0	3	0	0	0	0	0	0	0	0	0.231	0.832
N° of subst. Sites	1	1	0	0	7	0	0	0	0	0	0	0	0	0.692	1.932
N° privates subst. Sites	1	1	0	0	7	0	0	0	0	0	0	0	0	0.692	1.932
N° of indel sites	1	0	0	0	0	0	0	0	0	0	0	0	0	0.077	0.277
Pi	0.167	0.118	0	0	0.983	0	0	0	0	0	0	0	0	0.09751	0.27156

4. DISCUSSION

Phylogenetic analyzes based on the *rbc*L marker indicate that sea lettuce is molecularly represented by different species of the genus *Ulva.* Among 31 morphologically circumscribed species, 14 main molecular infragenerica taxa can be identified. Among all these taxa is observed some misidentifications, what reinforce that morphological plasticity and overlapping of diagnostic chacteristics produce a complex scenario, where molecular approaches should receive major attention in the definition of infrageneric taxonomy. The broad evaluation highlights the role of macroecological drivers, as temperature, in species segregations as in the case of *U. lactuca* and *U. fasciata/lactuca* complex*.* However, the wide, and sometimes disrupted distribution of some recently introduced species (HIRAOKA *et al.*, 2004), reinforce the importance of anthropogenic vectors in dispersion of some sea lettuce with higher ecophysiological plasticity, as those represented by *U. ohnoi* (WYNNE, 2011; MELTON III e LOPEZ-BAUTISTA, 2016).

The morphological plasticity of the genus was again confirmed, since individuals with different morphologies (Fig. A2) were sequenced in this study and grouped in the same clade *U. fasciata/lactuca* complex (Fig. 3). Evaluating the distribution of analyzed specimens of this clade, which include organisms identified as *U. fasciata*, *U. reticulata*, *U. rigida*, *U. rotundata* and *U. scandinavica* and *U. ohnoi*, it has been noted the predominance of representatives from Tropical regions (61 sequences) and Warm Temperate (27 sequences). However, there are also representatives in Temperate regions of the coast of Japan, Australia, New Zealand, Ireland and United Kingdom (total of 9 sequences) and Cold temperate in South Korea and Japan (total 2 sequences). *U. fasciata* Dellile, was named 1813, according to sampled material from Eastern Mediterranean (Egypt). The identification of *U. fasciata* in ballast waters of ships coming from Egyptian (Port Said) and Lebanese (Beirut) harbours reinforce the hypothesis that such taxon may have been favored by anthropogenic vectors to promote its dispersion (FLAGELLA *et al.*, 2010), giving it a cosmopolitan character. Herein we hypothesize that the broad distribution of this taxa, from tropical and warm temperate seas, should be considered as a consequence of natural but also, and especially, anthropogenic vectors. Indian ocean harbour a diverse population (Fig. 5), a potential source of propagule which now colonized many environments in different oceans. Similar patterns is observed in other macroalgae groups as the invader seaweed *Asparagopsis* which also in India have a site that represents higher genetic diversity, hosting both species (ANDREAKIS *et al.*, 2007).

Figure 5 – (a) Molecular diversity indexes (Theta ө S and π ± SD); (b) Matrix of coancestrality coefficients based on haplotype diversity among samples (Arlequin, output generate by R plugin)

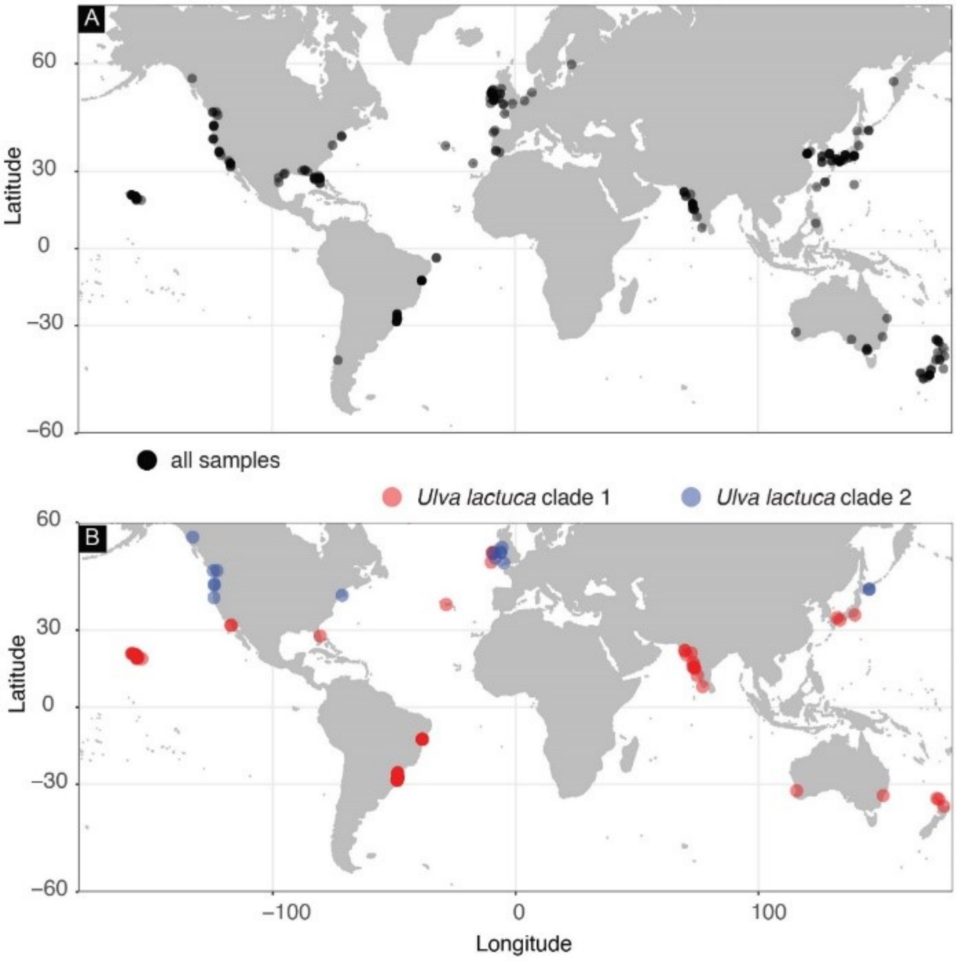


The proposition of Hawaiian *Ulva fasciata* as junior synonym of *U. lactuca* (O'KELLY et al., 2010), deserve further evaluations, as is still missed molecular characterization of type material. Based on this statement, specimens from India were treated as *U. lactuca*, despite their morphological features were consistent with the description of *U. fasciata* (KAZI *et al.*, 2016). However, these authors do not consider molecular characteristics of material from temperate regions. We suggest materials from both regions, Hawai and Indian coast, presented in the major clade, must be identified as *U. fasciata*, as in the segregation observed in the molecular characterization performed by (WAN *et al.*, 2017) and also adopted by (GUIDONE e THORNBER, 2013; KIRKENDALE *et al.*, 2013).

Therefore, the supposed cosmopolitanism of *U. lactuca*, previously based on morphological data, is now being questioned with the help of molecular data (HEESCH *et al.*, 2009). The clade majorly constituted by *Ulva lactuca*, with specimens from high latitudes, as the potential type locality in west coast of Sweden

(WOMERSLEY, 1985), suggest the monophyly of this taxa and a distribution limited to the north hemisphere. The notorious absence of *U. lactuca* in our research, as well as highlighted by other works on the south coast of Australia (KRAFT *et al.*, 2010; KIRKENDALE *et al.*, 2013), is important information for the clarification of the biogeography of this species. We emphasize that further studies are still necessary, mainly related the detailing of the molecular information of the type specimen. However, it is pertinent to point out the reports of *U. lactuca* on the coast of Brazil must be considered as synonyms of *U. fasciata.*

Figure 6 – Biogeographic distribution maps of sequences of the genus *Ulva*. In map (A), the black points correspond the distribution of all the sequences used in this work. In map (B), is shown the distribution of the two main clades, the clade 1 (red points) being with the largest number of sequences and clade 2 (blue points) mostly identified as *Ulva lactuca*.



On the other hand, we must highlight the cosmopolitanism of *U. fasciata.* Even though rbcL was considered a conservative marker, it was possible to observe the presence of 5 haplotypes from the subset of 99 *U. fasciata* sequences. Haplotype I present in all regions confirms the cosmopolitan nature of the species (Fig. 4). This may be a classic example of human activity-mediated dispersal since *Ulva* species are among the most problematic algal biofoulers transported around the world in the hulls and ballast water of ships (CALLOW *et al.*, 1997; LEWIS *et al.*, 2003; FLAGELLA *et al.*, 2007). In addition to this, rapid and massive growth, the reproduction alternatives (including fragmentation), and the opportunistic use of resources, contribute to the wide dispersion and ecological success of this species (KAMER e FONG, 2001; TAYLOR *et al.*, 2001; HEESCH *et al.*, 2009).

Although species of the genus have a fast and efficient response to environmental conditions, some molecular peculiarities show the influence of macroecological drivers in the speciation process, especially represented by temperature. Haplotype II and III are both observed in the Brazilian populations, with the former, however, restricted to the Tropical and the second to the Warm Temperate coast. The segregation of haplotypes in these biogeographic provinces, initially highlighted by HORTA *et al*., (2001) and revisited by SPALDING *et al*., (2007), have already been registered to other macroalalgal groups (SISSINI *et al.*, 2014b; GOUVÊA *et al.*, 2017). Thus, the relatively high genetic diversity observed in the Brazilian population of *U. fasciata* (please, see Pi values in Table 2) can be attributed to the relative isolation and oceanographic particularities which may have driven separately the evolution of southern (colder) and northeastern (warmer) populations. Temperature has been recognized as important environmental factor defining a physiological threshold for different *Ulva* species (MALTA *et al.*, 1999; NOTOYA, 1999) and should be played major role in *U. fasciata* adaptation. The presence of *U. fasciata* in ballast water (FLAGELLA *et al.*, 2010) fosters the hypothesis of an ancient but anthropogenic introduction (around the 1500's) in the south Atlantic. Further populational evaluation deserves special attention looking for a detailed molecular evaluation of its origins. This question will complement our knowledge about the role of first travelers in the human-induced beginnings of bioinvasion.

The detection of cryptic species of sea lettuce is of great importance considering that this group holds many species that can cause ecological imbalance and economic damages such as the formation of blooms and green tides (ANDREAKIS e SCHAFFELKE, 2012; MELTON *et al.*, 2016). Two samples of *Ulva* species collected in the Archipelago of Fernando de Noronha, Brazil coast, are strongly supported by a clade of *U. ohnoi* species identified in Japan, Hawaii, India and the United States, including the sequence of the haplotype of Japan [AB116040] (HIRAOKA *et al.*, 2004) (HIRAOKA et al., 2004).

Ulva reticulata, also present in this clade (Fig 3), is considered a sister species of *U. ohnoi*. In addition to genetic proximity, both have microscopic marginal teeth and a light green stem. However, the reproductive limit between species has been tested and there is no hybridization between *U. ohnoi* and *U. reticulata* (HIRAOKA *et al.*, 2004).

Human-mediated dispersion introduced many *Ulva* species into regions outside their natural geographical ranges (HEESCH *et al.*, 2009; HOFMANN *et al.*, 2010; WOLF *et al.*, 2012). *U. ohnoi* was first described in Japan (HIRAOKA *et al.*, 2004). Subsequently, it has been identified, based on molecular data, as a cryptic and invasive species for several works. In the Mediterranean, it was first reported by FLAGELLA *et al.*, (2010) as an algae introduced through ballast water. In the Western Atlantic, it was first reported in the Gulf of Mexico and the Atlantic coast of Florida, with samples collected during the formation of a green tide in July 2013 in Biscayne Bay (MELTON *et al.*, 2016). The species is also recognized for being responsible for the formation of green tides in warm temperate regions of southern and western Japan (HIRAOKA *et al.*, 2004).

The detection of *U. ohnoi* in a Brazilian Marine Protect Area (MPAs) represent an important alert for the arrival of cryptic alien species, that can impact autochtony diversity anonymously due their eventual invasive and opportunistic behavior (MELTON *et al.*, 2016). The record of non-native macroalgae species in the southwest Atlantic has become more frequent in recent years (AZEVEDO, CASSANO, JÚNIOR, BATISTA e DE OLIVEIRA, 2015; SISSINI *et al.*, 2016; BATISTA *et al.*, 2018). AZEVEDO *et al.*, (2015), recorded for the southern portion of Brazilian coast the occurrence of *Grateloupia turuturu* Yamada, a Pacific Ocean native species, considered the fifth most dangerous invasive seaweed (NYBERG e WALLENTINUS, 2005). The authors considered that the inlaying of boat hulls would be the most probable vector for such occurrence. Recently, BATISTA *et al.*, (2018) detected the arrival of rafts of Kelps-forming species from the sub-Antarctic region on the coast of Uruguay and southern Brazil. On this occasion, the authors corelated the dispersal of rafts to extreme climatic events, such as a strong extratropical cyclone occurred in September 2016 in the Southwest Atlantic. In Addition, the work of SISSINI *et al*., (2016) recorded the arrival of an unusual biomass of *Sargassum* floating on the northern edge of the Southern Atlantic. These floating masses were observed arriving in the Archipelago of Fernando de Noronha (03 ° 50'S, 32 ° 25'W), the same area where *U. ohnoi* samples were collected. On the occasion, authors related the phenomenon to a combination of factors involving changes in current patterns, in the seawater physicochemistry and biological interactions, which can facilitate propagule transport and invasion (SISSINI *et al.*, 2016). This scenario signalizes to the necessity for an international effort to synthesize molecular information of invasive species, as well transnational facility to evaluate target species that threat key environments around the world.

Our result reinforces the importance of molecular characterization of Ulva genus, as a major source of information in the taxonomical infrageneric evaluation. *U fasciata* represents the cosmopolitan sea lettuce observed in most of the Brazilian reefs. The minor but existent molecular differences between tropical and warm temperate population, suggest an ancient arrival. Molecular approach permitted the identification of *U. ohnoi* a possible recent bioinvasion in Fernando de Noronha Island, a key Brazilian MPA. Natural or even anthropogenic vector should be monitored regarding bioinvasion avoidance and coastal management, with special attention to MPAs.

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APPENDIX

Figura A1 – Maximum likelihood phylogenetic tree run with 1000 bootstraps based on 1141 bp of the chloroplast-encoded rbcL molecular marker.**Figura A1.** Maximum likelihood phylogenetic tree run with 1000 bootstraps based on 1141 bp of the chloroplast-encoded *rbc*L molecular marker.

Figure A2 – Representative images of morphological sampled types (*Ulva fasciata/lactuca*). A e B samples from Southwestern Atlantic (Santa Catarina's Island, Santa Catarina State, Brazil). C and D superficial cells. E and F cortical cells.

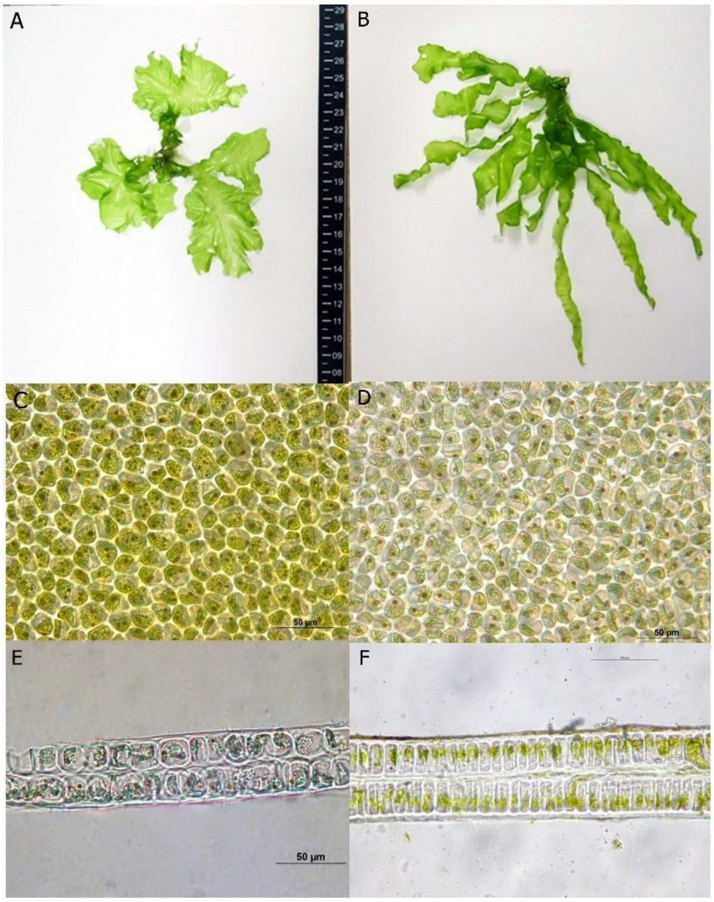

Table A1 – Measurements of the morphological characteristics considered to be diagnostic for *Ulva lactuca* and *Ulva fasciata* species. Measurements of the median region and thallus border.

	***Ulva lactuca* (A)**	***Ulva fasciata* (B)**
Fronde	**Expanded laminate**	**Laminating tape**
Cortical cells (diameter / length)	1,5-1,5μm	1,9 - 2,8μm
Surface cells (diameter / length)	17 -22μm	15 - 17μm
Pyrenoids presence	present	present

Figure A3 – Representative images of morphological samples of Ulva ohnoi collected in the archipelago of Fernando de Noronha, Brazil, and cultivated in laboratory. A) general appearance of the thallus; B) superficial view of the cells; C) superficial view of the cells; C) superficial view of the reproductive cells.

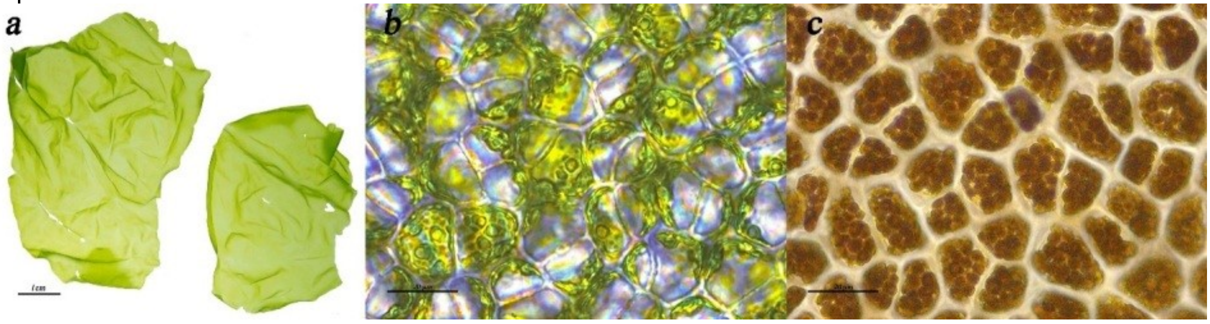

Tabela A2 – Collection site information of Ulva sp. with the GenBank Accession numbers and voucher numbers of the samples Brazil.

GenBank accession no						**Coordinates**	
Voucher ID	**Species**	**State**	**Country**	**Biogeographic Region**	**Ecoregion**	**Y**	**X**
U15_FSM_	*Ulva lactuca*	Bahia	Brazil	SWA	Warm Temperate	-28.60025	-48.817443
U10_PT_B	*Ulva lactuca*	Bahia	Brazil	SWA	Tropical	-13.009071	-38.461003
U11_PT_B	*Ulva lactuca*	Bahia	Brazil	SWA	Tropical	-13.009071	-38.461003
U12_PT_B	*Ulva lactuca*	Bahia	Brazil	SWA	Tropical	-13.009071	-38.461003
U13_PT_B	*Ulva lactuca*	Bahia	Brazil	SWA	Tropical	-13.009071	-38.461003
U14_PT_B	*Ulva lactuca*	Bahia	Brazil	SWA	Tropical	-13.009071	-38.461003
U15_PT_B	*Ulva lactuca*	Bahia	Brazil	SWA	Tropical	-13.009071	-38.461003
U16_PT_B	*Ulva lactuca*	Bahia	Brazil	SWA	Tropical	-13.009071	-38.461003
U17_PT_B	*Ulva lactuca*	Bahia	Brazil	SWA	Tropical	-13.009071	-38.461003
U18_PT_B	*Ulva lactuca*	Bahia	Brazil	SWA	Tropical	-13.009071	-38.461003
U19_PT_B	*Ulva lactuca*	Bahia	Brazil	SWA	Tropical	-13.009071	-38.461003
U2_PT_BA	*Ulva lactuca*	Bahia	Brazil	SWA	Tropical	-13.009071	-38.461003
U20_PT_B	*Ulva lactuca*	Bahia	Brazil	SWA	Tropical	-13.009071	-38.461003
U3_PT_BA	*Ulva lactuca*	Bahia	Brazil	SWA	Tropical	-13.009071	-38.461003
U4_PT_BA	*Ulva lactuca*	Bahia	Brazil	SWA	Tropical	-13.009071	-38.461003
U5_PT_BA	*Ulva lactuca*	Bahia	Brazil	SWA	Tropical	-13.009071	-38.461003
U6_PT_BA	*Ulva lactuca*	Bahia	Brazil	SWA	Tropical	-13.009071	-38.461003
U8_PT_BA	*Ulva lactuca*	Bahia	Brazil	SWA	Tropical	-13.009071	-38.461003
U1_Gua_P	*Ulva lactuca*	Paraná	Brazil	SWA	Warm Temperate	-25.888854	-48.562521
U2_Gua_P	*Ulva lactuca*	Paraná	Brazil	SWA	Warm Temperate	-25.888854	-48.562521

U3_GUA_P	*Ulva lactuca*	Paraná	Brazil	SWA	Warm Temperate	-25.888854	-48.562521
U4_GUA_P	*Ulva lactuca*	Paraná	Brazil	SWA	Warm Temperate	-25.888854	-48.562521
U7_FN_RN	*Ulva ohnoi*	Rio Grande do Norte	Brazil	SWA	Tropical	-3.834537	-32.397992
U8_FN_RN	*Ulva ohnoi*	Rio Grande do Norte	Brazil	SWA	Tropical	-3.83416	-32.397936
U1_FSM_SC	*Ulva lactuca*	Santa Catarina	Brazil	SWA	Warm Temperate	-28.60025	-48.817443
U2_FSM_S	*Ulva lactuca*	Santa Catarina	Brazil	SWA	Warm Temperate	-28.60025	-48.817443
U3_FSM_SC	*Ulva lactuca*	Santa Catarina	Brazil	SWA	Warm Temperate	-28.60025	-48.817443
U6_FSM_SC	*Ulva lactuca*	Santa Catarina	Brazil	SWA	Warm Temperate	-28.60025	-48.817443
U9_FSM_SC	*Ulva lactuca*	Santa Catarina	Brazil	SWA	Warm Temperate	-28.60025	-48.817443
UR_CLB_SC	*Ulva lactuca*	Santa Catarina	Brazil	SWA	Warm Temperate	-27.576341	-48.422945
U10_BL_SC	*Ulva lactuca*	Santa Catarina	Brazil	SWA	Warm Temperate	-27.574189	-48.420744
U14_BL_SC	*Ulva lactuca*	Santa Catarina	Brazil	SWA	Warm Temperate	-27.574189	-48.420744
U15_BL_SC	*Ulva lactuca*	Santa Catarina	Brazil	SWA	Warm Temperate	-27.574189	-48.420744
U18_BL_SC	*Ulva lactuca*	Santa Catarina	Brazil	SWA	Warm Temperate	-27.574189	-48.420744
U2_BL_SC	*Ulva lactuca*	Santa Catarina	Brazil	SWA	Warm	-27.574189	-48.420744

					Temperate		
U3_BL_SC	*Ulva lactuca*	Santa Catarina	Brazil	SWA	Warm Temperate	-27.574189	-48.420744
U4_BL_SC	*Ulva lactuca*	Santa Catarina	Brazil	SWA	Warm Temperate	-27.574189	-48.420744
U6_BL_SC	*Ulva lactuca*	Santa Catarina	Brazil	SWA	Warm Temperate	-27.574189	-48.420744
U8_BL_SC	*Ulva lactuca*	Santa Catarina	Brazil	SWA	Warm Temperate	-27.574189	-48.420744
U1_Taq_SC	*Ulva lactuca*	Santa Catarina	Brazil	SWA	Warm Temperate	-26.99509	-48.582456
U16_Taq_	*Ulva lactuca*	Santa Catarina	Brazil	SWA	Warm Temperate	-26.99509	-48.582456
U17_Taq_	*Ulva lactuca*	Santa Catarina	Brazil	SWA	Warm Temperate	-26.99509	-48.582456
U3_Taq_SC	*Ulva lactuca*	Santa Catarina	Brazil	SWA	Warm Temperate	-26.99509	-48.582456
U5_Taq_SC	*Ulva lactuca*	Santa Catarina	Brazil	SWA	Warm Temperate	-26.99509	-48.582456
U6_Taq_SC	*Ulva lactuca*	Santa Catarina	Brazil	SWA	Warm Temperate	-26.99509	-48.582456
U7_Taq_SC	*Ulva lactuca*	Santa Catarina	Brazil	SWA	Warm Temperate	-26.99509	-48.582456
U9_Taq_SC	*Ulva lactuca*	Santa Catarina	Brazil	SWA	Warm Temperate	-26.99509	-48.582456
AB097621	*Ulva arasakii*	Shizugawa, Miyagi Prefecture	Japan	NWP	Cold Temperate	38.668963	141.462663

EF109992	*Ulva armoricana*	South Island, Nelson	New Zealand	SWP	Temperate	-41.25813	173.28222
EF110294	*Ulva armoricana*	Karikari Peninsula, Northland	New Zealand	SWP	Temperate	-34.879774	173.382027
AB097630	*Ulva armoricana*	Brittany France	France	NEA	Temperate	48.131528	-4.279281
AB097631	*Ulva armoricana*	Hiroshima/Miyajima	Japan	NWP	Cold Temperate	34.262785	132.327783
AB097632	*Ulva armoricana*	Yokohama, Kanagawa, Japan	Japan	NWP	Cold Temperate	35.448428	139.651549
EF372236	*Ulva australis*	Coruña, Galicia	Spain	NEA	Temperate	42.792167	-8.910887
EU933953	*Ulva australis*	Flinders, VIC	Australia	SWP	Temperate	-38.471298	145.027033
EU933954	*Ulva australis*	Williamstown, VIC	Australia	SWP	Temperate	-37.85005	144.899941
EU933957	*Ulva australis*	Queenscliff, VIC	Australia	SWP	Temperate	-38.266515	144.649977
HM103371	*Ulva australis*	Sada	Espanha	NEA	Temperate	43.366685	-8.250013
KP975384	*Ulva australis*	Qingdao	China	NWP	Cold Temperate	36.046213	120.291003
HM142168	*Ulva beytensis*	Location not provided	?	?	?	?	?
AF499667	*Ulva californica*	Culture Collection_Location not provided	?	?	?	?	?
AY255866	*Ulva californica*	California	USA	NEP	Warm Temperate	32.832796	-117.28257
AY422555	*Ulva californica*	Oregon	USA	NEP	Cold Temperate	44.841894	-124.055161
AY422556	*Ulva californica*	California	USA	NEP	Cold Temperate	36.610068	-121.895037
AY422557	*Ulva californica*	California	USA	NEP	Cold Temperate	36.808265	-121.786748
AY422558	*Ulva californica*	Botany Bay, Vancouver Island	British Columbia	NEP	Cold Temperate	48.528333	-124.453361

AY422559	*Ulva californica*	California	USA	NEP	Cold Temperate	40.763343	-124.220025
AY422560	*Ulva californica*	California	USA	NEP	Cold Temperate	40.763343	-124.220027
EU484415	*Ulva californica*	Kerry	Ireland	NEA	Temperate	52.138346	-10.27694
KP233750	*Ulva californica*	Pohang	South Korea	NWP	Temperate	35.997815	129.568559
AB830528	*Ulva californica*	Kosai	Japan	NWP	Temperate	34.689969	137.579844
KC582341	*Ulva cf. lactuca*	Rhode Island	USA	NWA	Cold Temperate	41.493769	-71.39722
KC582350	*Ulva cf. rigida*	Rhode Island	USA	NWA	Cold Temperate	41.661944	-71.408684
EU484397	*Ulva compressa*	Galway	Ireland	NEA	Temperate	53.416667	-9.813349
AB097615	*Ulva compressa*	Yokohama, Kanagawa, Japan	Japan	NWP	Cold Temperate	35.300111	139.550442
AF189071	*Ulva curvata*	Lewes, Delaware Bay	USA	NWA	Cold Temperate	38.786217	-75.108976
KP233757	*Ulva fasciata*	California	USA	NEP	Warm Temperate	32.812591	-17.271053
KT882614	*Ulva fasciata*	Florida	USA	NWA	Tropical	27.85685	-80.445168
EU933962	*Ulva fasciata*	Point Peron, WA	Australia	SWP	Temperate	-32.273847	115.700528
AY422565	*Ulva fasciata*	Maui, Hawaii	Hawaii	EIP	Tropical	31.670369	-117.147211
HM454268	*Ulva fasciata*	India	India	WIP	Tropical	16.087838	72.991574
EF110501	*Ulva fasciata*	Pihakoa Point	India	WIP	Tropical	-34.879629	173.388189
AB097634	*Ulva fasciata*	Hiroshima/Miyajima	Japan	NWP	Cold Temperate	34.262785	132.327783
AB894323	*Ulva fasciata*	Kanagawa, Sajima, Tenjin-jima	Japan	NWP	Temperate	35.222149	139.609719
AB097633	*Ulva fasciata*	Kochi, Tosa	Japan	NWP	Temperate	33.449895	133.473023

EF110464	*Ulva fasciata*	North Island, Bay of Islands,Okahu Island	New Zealand	SWP	Temperate	-35.198825	174.205344
EF110500	*Ulva fasciata*	North Island, Coromandel, Wekarua	New Zealand	SWP	Temperate Cold	-37.448178	176.190591
KP233756	*Ulva fasciata*	Jeju	South Korea	NWP	Temperate	31.670371	-117.147213
EU484418	*Ulva fasciata*	Azores/Faial	Portugal	NEA	Temperate Cold	38.610928	-28.612184
AF499668	*Ulva fenestrata*	Washington	USA	NEP	Temperate	48.593168	-122.968411
HM447575	*Ulva flexuosa*	Tvärminne	Finland	BS	Temperate	59.845111	23.248411
AB097619	*Ulva flexuosa*	Wakayama Prefecture	Japan	NWP	Temperate	33.879753	135.14839
EU484402	*Ulva gigantea*	Galway	Ireland	NEA	Temperate	53.265623	-8.944994
EU484403	*Ulva gigantea*	Galway	Ireland	NEA	Temperate	53.265633	-8.944999
EU484414	*Ulva gigantea*	Cornwall	UK	NEA	Temperate	50.593725	-4.832704
AB097617	*Ulva intestinalis*	Karlskrona	Sweden	BS	Temperate	56.155526	15587261
AF387108	*Ulva lactuca*	Location not provided	?	?	?	?	?
AF499669	*Ulva lactuca*	Strangford Lough	Ireland	NEA	Temperate Cold	54.45801	-5.616827
AY422542	*Ulva lactuca*	Oregon	USA	NEP	Temperate Cold	44.499991	-124.083333
AY422543	*Ulva lactuca*	Vancouver	British Columbia	NEP	Temperate Cold	48.52593	-124.444533
AY422544	*Ulva lactuca*	Oregon	USA	NEP	Temperate Cold	44.84001	-124.053356
AY422545	*Ulva lactuca*	California	USA	NEP	Temperate Cold	40.76335	-124.22003
AY422546	*Ulva lactuca*	Alaska	Alaska	NEP	Temperate	56.813343	-132.96
EU484398	*Ulva lactuca*	Clare	Ireland	NEA	Temperate	53.158286	-9.118374

EU484399	*Ulva lactuca*	Dublin	Ireland	NEA	Temperate	53.286456	-6.109645
EU484400	*Ulva lactuca*	Dublin	Ireland	NEA	Temperate	53.28647	-6.10965
EU484409	*Ulva lactuca*	Cork	Ireland	NEA	Temperate	51.800028	-8.266667
EU484413	*Ulva lactuca*	Dorset	UK	NEA	Temperate	50.593634	-4.832584
AB097622	*Ulva lactuca*	Hokkaido	Japan	NWP	Cold Temperate	43.332836	145.574209
AB097623	*Ulva lactuca*	Hokkaido	Japan	NWP	Cold Temperate	43.33284	145.574202
KP279695	*Ulva lactuca*	Sidney	Australia	SWP	Temperate	-33913056	151276959
GU138239	*Ulva lactuca*	Kona	Hawaii	EIP	Tropical	19.672986	-156.026935
GU138292	*Ulva lactuca*	Mahukona	Hawaii	EIP	Tropical	20.186764	-155.90242
GU138271	*Ulva lactuca*	Kihei, Maui	Hawaii	EIP	Tropical	20.747466	-156.457992
GU138289	*Ulva lactuca*	Mahukona	Hawaii	EIP	Tropical	20.18114	-155.902109
GU138244	*Ulva lactuca*	Maui	Hawaii	EIP	Tropical	20.745751	-156.457715
GU138245	*Ulva lactuca*	Kihei, Maui	Hawaii	EIP	Tropical	20.764336	-156.459718
GU138258	*Ulva lactuca*	Kahului, Maui	Hawaii	EIP	Tropical	20.891418	-156.473271
GU138268	*Ulva lactuca*	Wailea, Maui	Hawaii	EIP	Tropical	20.689551	-156.443791
GU138246	*Ulva lactuca*	Ahihi Kinau, Maui	Hawaii	EIP	Tropical	20.600276	-156.422088
GU138259	*Ulva lactuca*	Kahului, Maui	Hawaii	EIP	Tropical	20.891735	-156.471961
GU138269	*Ulva lactuca*	Maalaea, Maui	Hawaii	EIP	Tropical	20.793138	-156.481773
GU138273	*Ulva lactuca*	Lahaina, Maui	Hawaii	EIP	Tropical	21.001537	-156.666587
GU138275	*Ulva lactuca*	Kalama Park, Maui	Hawaii	EIP	Tropical	20.730874	-156.453624
GU138276	*Ulva lactuca*	Puamana, Maui	Hawaii	EIP	Tropical	20.855268	-156.664351
GU138277	*Ulva lactuca*	Maluaka Beach, Maui	Hawaii	EIP	Tropical	20.600278	-156.441998
GU138278	*Ulva lactuca*	Maui	Hawaii	EIP	Tropical	20.862073	-156.149061
GU138282	*Ulva lactuca*	Polo Beach, Maui	Hawaii	EIP	Tropical	20.674353	-156.443892
GU138283	*Ulva lactuca*	Laupahoehoe	Hawaii	EIP	Tropical	19.986773	-155.234993

GU138285	*Ulva lactuca*	Lipoa St., Maui	Hawaii	EIP	Tropical	20.746995	-156.457946
GU138288	*Ulva lactuca*	Laaloa Bay Beach Park	Hawaii	EIP	Tropical	19.596061	-155.973352
GU138291	*Ulva lactuca*	Hookena Beach Park	Hawaii	EIP	Tropical	19.379521	-155.898327
GU138294	*Ulva lactuca*	Ualapue Fishpond, Molokai	Hawaii	EIP	Tropical	21.058152	-156.832527
GU138243	*Ulva lactuca*	Black Point, Oahu	Hawaii	EIP	Tropical	21.256512	-157.790677
GU138255	*Ulva lactuca*	Makai Pier, Oahu	Hawaii	EIP	Tropical	21.319924	-157.668984
GU138257	*Ulva lactuca*	Makai Pier, Oahu	Hawaii	EIP	Tropical	21.318963	-157.669423
GU138262	*Ulva lactuca*	Maili Beach Park, Oahu	Hawaii	EIP	Tropical	21.420073	-158.178682
GU138290	*Ulva lactuca*	Hookena Beach Park, Hawaii,	Hawaii	EIP	Tropical	19.378843	-153.897012
KP279687	*Ulva lactuca*	Adri, Gujarat	India	WIP	Tropical	20.955503	70.279527
KP279686	*Ulva lactuca*	Bhidbanjan, Gujarat	India	WIP	Tropical	21.547787	72.294051
KP279688	*Ulva lactuca*	Harihareshwar, Maharashtra	India	WIP	Tropical	17.989678	73.021141
KP279691	*Ulva lactuca*	Malvan, Maharashtra	India	WIP	Tropical	16.060028	73.454621
KP279690	*Ulva lactuca*	Redi, Maharashtra	India	WIP	Tropical	15.731831	73.667233
KP279694	*Ulva lactuca*	Ullal, Karnataka	India	WIP	Tropical	12.802384	74.842214
KP279692	*Ulva lactuca*	Vagathor, Goa	India	WIP	Tropical	15.609379	73.732191
KP279693	*Ulva lactuca*	Vizhinjam, Kerala	India	WIP	Tropical	8394633	76.969349
EU933943	*Ulva laetevirens*	Williamstown, Melbourne	Australia	SWP	Temperate	-37.866664	144.883335
EU933961	*Ulva laetevirens*	Adelaide, SA	Australia	SWP	Temperate	-34.831002	138.479927
AB830525	*Ulva limnetica*	Mikata-goko	Japan	NWP	Cold Temperate	35.612778	135.891678
DQ813496	*Ulva linza*	Stewart Island, Port William	New Zealand	SWP	Subantarctic	-46.836654	168.088561
EF110016	*Ulva linza*	Stewart Island, Port William	New Zealand	SWP	Subantarctic	-46.844972	168.082986
EF110386	*Ulva linza*	Chatham Islands, Owenga	New Zealand	SWP	Temperate	-44.017129	176.386658
FM210341	*Ulva linza*	Shandong province,Qingdao	China	NWP	Cold Temperate	36.060598	120.319819
FM210344	*Ulva linza*	Algarve	Portugal	NEA	Temperate	37.009992	-7.770185

HM046607	*Ulva linza*	Qingdao	China	NWP	Cold Temperate	36.05078	120.490789
HM584749	*Ulva linza*	Zhanqiao, Qingdaoa	China	NWP	Cold Temperate	36.061544	120.312215
HM584751	*Ulva linza*	Zhanqiao, Qingdaoa	China	NWP	Cold Temperate	36.06155	120.312212
KP233762	*Ulva linza*	Pohang	South Korea	NWP	Cold Temperate	36.05602	129.378164
KP233763	*Ulva linza*	Jeju	South Korea	NWP	Cold Temperate	33.229132	126.314431
KP233764	*Ulva linza*	Muan	South Korea	NWP	Cold Temperate	35.149418	126.33062
KP233765	*Ulva linza*	Qingdao, Shandong	China	NWP	Cold Temperate	36.056039	120.337445
KP233766	*Ulva linza*	Qingdao, Shandong	China	NWP	Cold Temperate	36.056039	120.337445
AB097620	*Ulva linza*	Tokushima	Japan	NWP	Warm Temperate	34.084505	134.6036
AB741533	*Ulva linza*	Hokkaido	Japan	NWP	Cold Temperate	43.205931	140.877924
AB830520	*Ulva linza*	Fukui	Japan	NWP	Cold Temperate	35.610065	135.889989
AY255868	*Ulva lobata*	Oregon	USA	NEP	Cold Temperate	44.626037	-124.068098
AY422550	*Ulva lobata*	California	USA	NEP	Warm Temperate	35.61503	-121.149978
AY422563	*Ulva muscoides*	Cadiz	Spain	NEA	Temperate	36.499995	-6.333497

KJ417451	*Ulva mutabilis*	Lagoon Ria Formosa	Portugal	NEA	Temperate	37.011207	-7.998312
GU138241	*Ulva ohnoi*	HI, Maui Island	Hawaii	EIP	Tropical	20.923263	-156.492958
GU138250	*Ulva ohnoi*	HI, Oahu Island	Hawaii	EIP	Tropical	21.256468	-157.790598
KP279702	*Ulva ohnoi*	Circuit House, Veraval, Gujarat	India	WIP	Tropical	20.899934	70.369165
KP279696	*Ulva ohnoi*	Harihareshwar, Maharashtra	India	WIP	Tropical	17.991565	73.028973
KP279704	*Ulva ohnoi*	Harihareshwar, Maharashtra	India	WIP	Tropical	17.991565	73.028973
KP279700	*Ulva ohnoi*	Kolthare, Maharashtra	India	WIP	Tropical	17.991565	73.028973
KP279699	*Ulva ohnoi*	Ladghar, Maharashtra	India	WIP	Tropical	17.720183	73.133505
KP279703	*Ulva ohnoi*	Ladghar, Maharashtra	India	WIP	Tropical	17.720183	73.133505
KP279697	*Ulva ohnoi*	Palshet, Maharashtra	India	WIP	Tropical	17.442492	73.192312
KP279698	*Ulva ohnoi*	Panchanadi, Maharashtra	India	WIP	Tropical	17.644027	73.133853
KP279701	*Ulva ohnoi*	Purngad, Maharashtra	India	WIP	Tropical	16806057	73311051
AB116039	*Ulva ohnoi*	Fukuoka, Fukuoka	Japan	NWP	Temperate	33.612898	130.398423
AB116037	*Ulva ohnoi*	Kochi, Tosa	Japan	NWP	Temperate	33.514971	133.7752248
AB116038	*Ulva ohnoi*	Kochi, Tosa	Japan	NWP	Temperate	33.514971	133.7752248
AB116040	*Ulva ohnoi*	Kochi, Tosa	Japan	NWP	Temperate	33.514971	133.7752248
AB116035	*Ulva ohnoi*	Okinawa, Naha	Japan	NWP	Temperate	26.222241	127.668283
AB116036	*Ulva ohnoi*	Okinawa, Naha	Japan	NWP	Temperate	26.222241	127.668283
KU561282	*Ulva ohnoi*	Bradenton, FL	USA	NWA	Tropical	27.5323889	-82.6466667
KU561290	*Ulva ohnoi*	Cocoa, FL	USA	NWA	Tropical	28.3556389	-80.7208333
KU561287	*Ulva ohnoi*	Corpus Christi Bay, Corpus Christi, TX	USA	NWA	Tropical	27.7875	-97.3916667
KU561285	*Ulva ohnoi*	Deering Estate, Biscayne Bay, FL	USA	NWA	Tropical	25.6161111	-80.3052778
KU561296	*Ulva ohnoi*	Destin, FL	USA	NWA	Tropical	30.3864167	-86.515
KU561299	*Ulva ohnoi*	Destin, FL	USA	NWA	Tropical	30.3864167	-86.515

KU561288	*Ulva ohnoi*	Fort Pierce, FL	USA	NWA	Tropical	27.4709167	-80.2894444
KU561293	*Ulva ohnoi*	Fort Pierce, FL	USA	NWA	Tropical	27.4730833	-80.3227778
KU561294	*Ulva ohnoi*	Fort Pierce, FL	USA	NWA	Tropical	27.4736111	-80.3225
KU561295	*Ulva ohnoi*	Fort Pierce, FL	USA	NWA	Tropical	27.4736111	-80.3225
KU561298	*Ulva ohnoi*	Freeport Harbor Channel, Surfside Beach, TX	USA	NWA	Tropical	28.9368056	-95.295
KU561286	*Ulva ohnoi*	Galveston Jetty, Galveston, TX	USA	NWA	Tropical	29.3313611	-94.7233333
KU561279	*Ulva ohnoi*	Perdido Pass, Orange Beach, ALABAMA	USA	NWA	Tropical	30.2743056	-87.5594444
KU561280	*Ulva ohnoi*	Port Isabel, TX	USA	NWA	Tropical	26.0779722	-97.2058333
KU561297	*Ulva ohnoi*	Saint Joseph Bay, Port St. Joe, FL	USA	NWA	Tropical	29.810302	-85.30558
KU561289	*Ulva ohnoi*	Siesta Key, FL	USA	NWA	Tropical	27.2468056	-82.5361111
KU561284	*Ulva ohnoi*	Tampa Bay, FL	USA	NWA	Tropical	27.8578333	-82.5516667
KU561283	*Ulva ohnoi*	Tampa Bay, FL	USA	NWA	Tropical	27.8906667	-82.5388889
KU561292	*Ulva ohnoi*	Venice Jetty, Venice, FL	USA	NWA	Tropical	27.1137222	-82.4661111
KU561291	*Ulva ohnoi*	Watson Island, Miami, FL	USA	NWA	Tropical	25.7840278	-80.1725
AB894324	*Ulva pertusa*	Kanagawa, Sajima, Tenjin-jima	Japan	NWP	Temperate	25.222024	139.603031
AY422547	*Ulva pertusa*	California	USA	NEP	Warm Temperate	32.767264	-117.229911
AY422548	*Ulva pertusa*	California	USA	NEP	Warm Temperate	32.815091	-117.273566
EF110096	*Ulva pertusa*	North Island, Taranaki	New Zealand	SWP	Temperate	-39.0558	174.035
EF110121	*Ulva pertusa*	South Island, Dunedin	New Zealand	SWP	Temperate	-45.880036	170.513
EF110154	*Ulva pertusa*	North Island, Wellington	New Zealand	SWP	Temperate	-41.30017	174.831967
EF110189	*Ulva pertusa*	North Island, Northland, Whangarei	New Zealand	SWP	Temperate	-35.834972	174.5727
EF110270	*Ulva pertusa*	South Island, Fiordland	New Zealand	SWP	Temperate	-45.284181	166.897974
HM584759	*Ulva pertusa*	Qingdao	China	NWP	Cold	36.056976	120.335379

					Temperate		
HM584760	*Ulva pertusa*	Qingdao	China	NWP	Cold Temperate	36.051246	120.360982
HM584767	*Ulva pertusa*	Rushan, Weihai	China	NWP	Cold Temperate	36.822304	121.662563
KP233767	*Ulva pertusa*	Bukbu Beach, Pohang	China	NWP	Cold Temperate	36.014478	129.397222
KP233768	*Ulva pertusa*	Songseok-ri, Haeje-myeon, Muan	South Korea	NWP	Cold Temperate	35.144995	126.32997
KP233769	*Ulva pertusa*	Jeju	South Korea	NWP	Cold Temperate	33.232333	126.313847
AB097624	*Ulva pertusa*	Kochi	Japan	NWP	Warm Temperate	33.44902	133.442572
AB097625	*Ulva pertusa*	Fukuoka, Hakata	Japan	NWP	Warm Temperate	33.603838	130.380184
AB097626	*Ulva pertusa*	Hiroshima, Miyajima	Japan	NWP	Temperate	34.290381	132.299029
AB097627	*Ulva pertusa*	Kanagawa, Yokohama	Japan	NWP	Temperate	35.45143	139.657111
AB097628	*Ulva pertusa*	Mikawa, Aichi	Japan	NWP	Temperate	34.771337	137.168071
HM584770	*Ulva prolifera*	Qingdao	China	NWP	Cold Temperate	36.050928	120.351633
AB598810	*Ulva prolifera*	Ishigaki Island, Okinawa	Japan	NWP	Warm Temperate	24.355311	124.213061
AY422553	*Ulva pseudocurvata*	California	USA	NEP	Warm Temperate	33.625065	-117.893344
HQ026496	*Ulva reticulata*	Location not provided	?	?	?	?	?
AB097635	*Ulva reticulata*	Cebu Island	Philippines	CIP	Tropical	10.236834	123.824611
AY422568	*Ulva reticulata*	Kihei, Maui	Hawaii	EIP	Tropical	20.783333	-156.466657

KC661464	*Ulva reticulata*	Kalubhar Island	India	WIP	Tropical	22.483336	69.616884
KC661462	*Ulva reticulata*	Kalubhar Island,	India	WIP	Tropical	22.483336	69.616884
KC661463	*Ulva reticulata*	Kalubhar Island,	India	WIP	Tropical	22.483336	69.616884
AY422564	*Ulva rigida*	Puerto Montt	Chile	SEP	Temperate	-41.473082	-72.93933
EF109941	*Ulva rigida*	South Island, Otago	New Zealand	SWP	Temperate	-45.795417	170.656498
EF109942	*Ulva rigida*	South Island, Otago	New Zealand	SWP	Temperate	-45.795417	170.656498
EF109953	*Ulva rigida*	Tirohanga	New Zealand	SWP	Temperate	-46.435654	169.797227
EF109974	*Ulva rigida*	Papanui Inlet, Otago Peninsula	New Zealand	SWP	Temperate	-45.848772	170.709422
EF110004	*Ulva rigida*	Timaru, North Mole	New Zealand	SWP	Temperate	-44.384963	171.258974
EF110116	*Ulva rigida*	South Island, Timaru	New Zealand	SWP	Temperate	-44.391406	171.260021
EF110275	*Ulva rigida*	Fiordland	New Zealand	SWP	Temperate	-45.284107	166.89796
EF110302	*Ulva rigida*	North Island, Wellington	New Zealand	SWP	Temperate	-41.342282	174.81853
EU484408	*Ulva rigida*	Galway	Ireland	NEA	Temperate	53.605724	-9.8088532
EU484417	*Ulva rigida*	Kilmore Quay	Ireland	NEA	Temperate	52.150013	-6.583313
HG940504	*Ulva rigida*	Cork, Clonakilty	Ireland	NEA	Temperate	51.595892	-8.860535
HG940506	*Ulva rigida*	Waterford, Dungarvan	Ireland	NEA	Temperate	52.070008	-7.619895
HG940507	*Ulva rigida*	Mayo, Moy Estuary	Ireland	NEA	Temperate	54.190017	-9.149975
HG940509	*Ulva rigida*	Mayo, Moy Estuary	Ireland	NEA	Temperate	54.190009	-9.150048
HG940510	*Ulva rigida*	Cork, Courtmacsherry	Ireland	NEA	Temperate	51.635626	-8.719029
HG940511	*Ulva rigida*	County Mayo, Murrisk	Ireland	NEA	Temperate	53.782189	-9.64171
KP233772	*Ulva rigida*	Pohang	South Korea	NWP	Cold Temperate	35.99738	129.566565
KP975386	*Ulva rigida*	Shandong province, Qingdao	China	NWP	Cold Temperate	36.060715	120.381007
LK022428	*Ulva rigida*	Otago Harbour	New Zealand	SWP	Temperate	-45.799972	170.700013
LK939140	*Ulva rigida*	Zeeland, Lake Veere	Netherlands	NEA	Temperate	51.550571	3.88918
EU484395	*Ulva rigida*	Inis Mor, Aran Islands	Ireland	NEA	Temperate	53.098674	-9.58715133

EU484401	*Ulva rotundata*	Galway	Ireland	NEA	Temperate	53.288231	-9.558318
EU484404	*Ulva rotundata*	Galway	Ireland	NEA	Temperate	53.416722	-9.814984
EU484406	*Ulva rotundata*	Clare	Ireland	NEA	Temperate	53.119974	-9.15324
HG940508	*Ulva rotundata*	Clare	Ireland	NEA	Temperate	53.156406	-9.071518
EU484396	*Ulva rotundata*	Casla, Co. Galway	Ireland	NEA	Temperate	53284718	-9554145
AY255870	*Ulva scandinavica*	Portsmouth	United Kingdom	NEA	Temperate	50.766366	-1.066969
EU484416	*Ulva scandinavica*	Cork	Ireland	NEA	Temperate	51.650019	-8.678378
AB097629	*Ulva scandinavica*	Wadden Sea	Netherlands	NEA	Temperate	53.57773	6.949294
EU484412	*Ulva scandinavica*	Langstone Harbour, Hampshire	United Kingdom	NEA	Temperate	50821796	-1005091
AB830517	*Ulva simplex*	Fukui	Japan	NWP	Cold Temperate	35.622041	135.896881
EF110308	*Ulva sp.*	North Island, Northern Wairarapa	New Zealand	SWP	Temperate	-40.219898	176.78
EF110468	*Ulva sp.*	North Island, Bay of Islands	New Zealand	SWP	Temperate	-35.242454	174.117989
AB097636	*Ulva spinulosa*	Kochi, Fubenhama	Japan	NWP	Warm Temperate	33.491418	133.560213
AY255874	*Ulva stenophylla*	Oregon	USA	NEP	Cold Temperate	47.689797	-122.403579
AY255875	*Ulva taeniata*	California	USA	NEP	Cold Temperate	36.627126	-121.918181
AY422566	*Ulva taeniata*	California	USA	NEP	Warm Temperate	32.695002	-117.25503
AY422567	*Ulva taeniata*	California	USA	NEP	Warm Temperate	32.695002	-117.25503
AB894325	*Ulva tanneri*	Kanagawa, Sajima	Japan	NWP	Warm Temperate	35.222235	139.602793

AF499672	*Ulva tanneri*	California	USA	NEP	Warm Temperate	36.610037	-121.895
EU933944	*Ulva tanneri*	Brisbane	Australia	SWP	Temperate	-27.401501	153.170573
AB830519	*Ulva torta*	Fukui, Mihama	Japan	NWP	Cold Temperate	35.610009	135.89
EF110112	*Umbraulva olivascens*	South Island, Timaru	New Zealand	SWP	Temperate	-44.391916	171.259688
EU484405	*Umbraulva olivascens*	Carna, Co. Galway	Ireland	N_A	Temperate	53.316546	-9.833349

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CAPÍTULO 2

KELPS' LONG-DISTANCE DISPERSAL: ROLE OF ECOLOGICAL/OCEANOGRAPHIC PROCESSES AND IMPLICATIONS TO MARINE FOREST CONSERVATION

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Kelps' Long-Distance Dispersal: Role of Ecological/Oceanographic Processes and Implications to Marine Forest Conservation

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ABSTRACT

Long-distance dispersal is one of the main drivers structuring the distribution of marine biodiversity. This study reports the first occurrence of *Macrocystis pyrifera* and *Durvillaea antarctica* rafts on the southwestern warm temperate coast of the Atlantic Ocean. Our results indicate that an extreme meteo-oceanographic event, characterized by a northward, displacement of cold sub-Antarctic oceanic waters driven by an extratropical cyclone, could account for these unusual occurrences. A niche model based on known current distribution and maximum entropy principle (MAXENT), revealed the availability of suitable habitats at lower latitudes, outside their actual distribution edges. The distributional boundaries, mainly driven by temperature and irradiance, suggest the existence of environmental suitability in warm temperate areas, as well as in the Northern Hemisphere off Atlantic and Asian coasts. These theoretical edges and respective environmental drivers agree with the physiological affinities of both species, supporting the hypothesis that these variables act as limiting factors for their occurrences in tropical or warmer areas. Emerging regions can function as refuges and stepping-stones, providing substrate with adequate habitat conditions for recruitment of propagules, allowing eventual colonization. Long dispersal events reinforce the need for an extensive discussion on selective management of natural dispersion, biological invasions, refuge mapping and conservation initiatives in a transnational perspective.

Keywords: Kelp rafts; marine migration; niche model; biogeography; upwelling; extratropical cyclone.

1 INTRODUCTION

The dispersal of marine organisms is one of the main ecological and evolutionary drivers of marine biodiversity composition and structure, with currents representing one of the principal players in these processes (JACKSON e SAX, 2010; MACARTHUR e WILSON, 2015; PINHEIRO *et al.*, 2017). Currents can influence the range of dispersal of migrant populations, promote connectivity, and assist in the process of finding suitable habitats (MACKAS *et al.*, 1985; GAYLORD e GAINES, 2000; GILG e HILBISH, 2003; ZAKAS *et al.*, 2009). Besides providing transport, currents also play a role in determining niche characteristics, limiting physiological and developmental processes, that require specific abiotic conditions such as temperatures, salinity, and nutrient concentrations (BROWN e MAURER, 1989; BROWN, 1995). Such aspects have been receiving more attention in recent years due to climate change. Global warming is producing critical changes in ocean circulation patterns, niche availability and characteristics, and biodiversity redistribution (BEAL *et al.*, 2011; O'GORMAN, 2016). At the same time, changes in global ocean circulation patterns can interact locally with specific regional climatic conditions. In the South Atlantic more frequent and intense storms have been observed in recent decades, which compromise oceanic circulation and migration processes (KNUTSON *et al.*, 2010; COUMOU e RAHMSTORF, 2012; SISSINI *et al.*, 2014a). Currents acting together with storm-winds are efficient dispersal mechanisms for floating strategists and associated communities. One such community affected by storms is kelp forests (EASTERLING *et al.*, 2000; MACARTHUR e WILSON, 2015).

During storms, kelps get detached from the substrate. Many of the detached plants become entangled in other detached kelp plants and eventually form what are called kelp rafts (CHEN *et al.*, 2011). These floating masses, sometimes abundant and with a diversified fauna and flora, can be transported rapidly and beyond their distributional boundaries (EASTERLING *et al.*, 2000; CHEN *et al.*, 2011; MACARTHUR e WILSON, 2015). Oceanographic/climatic events can work together to transport an entire specimen, or kelp rafts, with potentially viable propagules, to suitable far-off niches. However, effective species establishment will depend on a combination of abiotic and biotic conditions, which will be influenced by the settlement of the juveniles and the development of the propagules (TEGNER *et al.*, 1997; PEARSON e DAWSON, 2003; ANDERSON *et al.*, 2017).

Density dependent mechanisms, such as competition, predation, and herbivory, represent additional dispersal and developmental barriers in marine environments (GARBARY, 2001; SOBERÓN e NAKAMURA, 2009; MACARTHUR e WILSON, 2015). However, specific benthic organisms or community structure can change micro niche conditions, facilitating settlement and development of invertebrates and primary producers (BRUNO *et al.*, 2003; THOMSEN e MCGLATHERY, 2005).

The combination of all these physico-chemical and biological processes will produce the realized niche, which can be recognized as the space currently occupied by a species, after the migratory and selective pressures imposed by positive and negative biological interactions. This is distinct from the fundamental niche (HUTCHINSON, 1957; DAYTON e TEGNER, 1984; BROWN, 1995; TEGNER *et al.*, 1997; DAYTON *et al.*, 1999; ELITH e LEATHWICK, 2009), where the range of environmental conditions within which a species has a suitable habitat (i.e., can in theory survive and persist),but might not occur there due to biological interactions or processes such as competitive exclusion or limited migration. These concepts were refined by Hutchinson (1957), who hypothesized that the fundamental niche could be mapped in physical space, thus predicting where species should be able to live. The effectiveness of niche modeling tools provides support to Hutchinson's assumptions (PETERSON e VIEGLAIS, 2001; TYBERGHEIN *et al.*, 2012a). Nowadays, species distribution models are recognized as an important tool to determine niche suitability for marine organisms, particularly macroalgae, in contemporary climatic and oceanographic spaces (GRAHAM *et al.*, 2007; VERBRUGGEN *et al.*, 2007; GOTELLI e STANTON-GEDDES, 2015; ASSIS, V. D. L. *et al.*, 2016).

Macroalgae play a key role in different marine environments, sometimes building biogenic reefs or underwater forests. These organisms influence and create niches, which represent, food, shelter and substrate for a high diversity of marine organisms, especially in temperate environments (HIGHSMITH, 1985; STENECK *et al.*, 2003). Kelp forest ecosystems are among the largest biogenic structures found in the benthic marine system (DAYTON, 1985). Primary producers were recognized even by ancient naturalists like Charles Darwin, who emphasized the fundamental ecological importance of these subtidal forests in high latitudes of South America (DARWIN, 1871). These environments are considered common and abundant in temperate and sub-Antarctic regions (MACAYA e ZUCCARELLO, 2010; GRIFFITHS e WALLER, 2016).

One of the dominant species of kelp forests is *Macrocystis pyrifera* (Linnaeus) *C.* Agardh, commonly known as giant kelp. It occurs in both the Northern Hemisphere (western coast of North America) and the Southern Hemisphere (i.e., Australia, New Zealand, South Africa, sub-Antarctic islands, and the western and eastern coasts of South America) (GRAHAM *et al.*, 2007). In the Southern Atlantic, along the east coast of South America, its northernmost boundary is the northern region of Argentinean Patagonia, Craker Bay (42°56′ S 64°27′ W) (KUHNEMANN, 1970; RAFFO *et al.*, 2009). Molecular and fossil characterization indicates that this taxon originates in the North American Pacific Coast, migrating to the Southern Hemisphere 10,000 yr ago, during a colder period. Similar North to South migrations have been hypothesized in the Atlantic Ocean (ROTHMAN *et al.*, 2017). The ancestor of both *Laminaria abyssalis* A.B. Joly & E.C. Oliveira and *L. pallida* Greville, originated in the Northern Hemisphere and migrated south during cold periods.

Kelps have a biphasic life cycle. Ladah & Zertuche-Gonzales (2007) showed that *Macrocystis* can survive long periods in its microscopic forms (gametophytes), which would enable it to survive under warmer conditions in a seed bank analogue turf environment. Interestingly, it has been suggested that vegetative propagation of these undifferentiated filamentous haploid forms can have contributed to antitropical east Pacific distribution (WESTERMEIER *et al.*, 2011). Once the conditions become favorable, the gametophytes would continue its life cycle to form the macroscopic thallus (sporophytes) (LADAH e ZERTUCHE-GONZÁLEZ, 2007). The sporophytes of *Macrocystis pyrifera* can grow up to 30 m in length, on a hard substrate, while it is kept erect in the water column by aerenchyma or floater vesicles, which also facilitate dispersal (MACAYA *et al.*, 2005; HERNÁNDEZ-CARMONA *et al.*, 2006). They form large floating patches or “rafts” that can travel long distances for a long period of time (i.e., over three months), with their reproductive capacity still viable (MACAYA *et al.*, 2005).

The distribution of *Durvillea antarctica* (Chamisso) Hariot is limited to the Southern Hemisphere (HAY, 1994; GRAHAM *et al.*, 2007). It has a diplontic life cycle. Despite the absence of an alternate phase in the life cycle, this species can remain afloat for more than one month (because of the presence of aerenchyma) in cool water and low irradiance, typical conditions for winter and part of spring or fall.

Temperatures of up to 17 °C, combined with higher irradiance during summer (maximal values 16.1–21.8 W m^{-2}) were correlated with significant biomass losses and rapid destruction of *Durvillea* rafts (LADAH e ZERTUCHE-GONZÁLEZ, 2007). However, some kelp populations have colonized habitats with higher temperatures and irradiances, at lower latitudes, such as those that were observed at the western shores of southern California to Mexico, northern Chile to Peru, south-western South Africa and western Australia (CASTAÑEDA e REYES-BONILLA, 2010). In such cases, despite the relatively lower latitude, environments are influenced by nutrient-rich upwelled waters or cold eastern boundary currents that flow towards the Equator (STENECK *et al.*, 2003; CASTAÑEDA e REYES-BONILLA, 2010). The few kelp species that occur in tropical environments have their distributions restricted to deeper zones within the photic zone, where light and nutrients are sufficient for their growth (GRAHAM *et al.*, 2007). *Laminaria abyssalis*, an endemic to the Brazilian coast, is an example of a tropical kelp. This species occurs at depths of between 40–115 m, and uses rhodolith beds as a substrate (MARINS *et al.*, 2014).

Tropical kelp forests are considered relict species from an immigration of shallow water populations. During the Pleistocene some populations expanded their distributional boundaries to lower latitudes due to the lower Atlantic temperatures, that in these equatorial regions were up to 5 °C below the mean values observed in the surface during the last decade (EMILIANI, 1955; LÜNING, 1990). Presently, climatic projections suggest potential changes in species distribution (BELLARD *et al.*, 2012), especially for subtidal kelps, which are vulnerable to sea surface temperature (SST) changes, due to their affinities with cold water (LÜNING, 1990). Losses of kelp forests' distributional ranges are reported in various regions of the world (SCHIEL e FOSTER, 2006; FERNÁNDEZ, 2011; ASSIS, V. D. L. *et al.*, 2016). The reduction of *Saccorhiza polyschides* (Lightfoot) Batters and *Laminaria hyperborea* (Gunnerus) Foslie populations on the northern coast of Spain was related to the increase in SST and the reduction of upwelling intensity in the region (FERNÁNDEZ, 2011). However, regional cooling has been observed in coastal areas of South America (FALVEY e GARREAUD, 2009) and South Africa (BOLTON *et al.*, 2012). In South Africa, this resulted in the extension of the known distribution limits of *Ecklonia maxima* (Osbeck) Papenfuss. Some studies suggest that kelp may find refuge in deeper environments, far from the general warming tendency of oceanic surface waters (GRAHAM *et al.*, 2007; ASSIS, V. D. L. *et al.*, 2016). Thus, the existence of temperate algae refuges, even in tropical or warm temperate environments, is of extreme relevance, not only for understanding biogeographic patterns, but for conservation purposes also. Graham et al., (2007) modeled deep-water kelp refugia, and with the use of the model's predictions they have discovered dense and extensive populations of *Eisenia galapagensis* in deep waters of the Galapagos archipelago. Although modeling constitutes an essential tool for the discussion of marine macroecological processes (VERBRUGGEN *et al.*, 2009b), there are no published articles with models predicting niche habitat suitability for *M. pyrifera* and *D. antarctica,* two of the most important kelp species.

Therefore, better understandings of ecological and evolutionary mechanisms would contribute to the comprehension of key population dynamic and resilience. The definition of target foundation species or groups and mapping niche suitability may improve management, when considering future needs for biodiversity management or conservation (PALUMBI *et al.*, 2003; ANDERSON *et al.*, 2014). Differentiating natural drift-refuge colonization process from anthropogenic transport-bioinvasion process is a crucial task (SHEFER *et al.*, 2004). This aspect reinforces discussion about large scale dispersal in an eco-evolutionary framework (FACON *et al.*, 2006) and should influence stakeholder decision regarding the necessity of conservationist intervention or complete eradication of a migrant target population (SHEFER *et al.*, 2004; FACON *et al.*, 2006).

Here we report (1) the first observation of rafts of two kelp species (*M. pyrifera* and *D. Antarctica*) on the Brazilian and Uruguayan coasts; (2) provides the general physiological state of immigrant specimens; (3) discusses the possible origin of these rafts; (4) and model both species habitat suitability considering dispersion routs, potential settlement and colonization on a global scale. Moreover, we characterize the oceanographic processes that caused this dispersal event and discuss implications of these dispersal events considering coastal management and conservation.

2. MATERIALS AND METHODS

2.1. Study Area

The kelp rafts were found along the beach of Campeche in Florianópolis (27°39′23.21″ S; 48°28′13.13″ W), Santa Catarina State, southern Brazil, and the beaches of La Paloma, Punta del Diablo, Santa Teresa, La Coronilla and Barra del Chuy, Uruguay (between 33°38′58.58″ S; 53°27′58.03″ W and 34°39′52.5″ S; 54°10′0″ W). The continental shelf off this region is located near the Brazil-Malvinas Confluence (BMC) region, located at 38° S ± 2° (ANDERSON *et al.*, 2014; ANDERSON *et al.*, 2015). The Falkland Current (Malvinas Current) acts as a branch of the sub-Antarctic Front, which is the northernmost oceanographic process associated with the Antarctic Circumpolar Current in the Drake Passage (OLSON e RICHARDS, 1988). These cold, sub-Antarctic water masses flow from the south northwards and meet the warmer and more saline waters from the Brazil Current, between latitudes 36° and 39° S giving rise to the Subtropical Convergence (PETERSON e STRAMMA, 1991). This is also where the South Atlantic Central Water (SACW) current is formed (Figure 1). The nutrient rich, low temperature current intrudes the shallower strata near the continental shelf and is responsible for the common upwelling phenomena, over a 27 km section of the coast (PEREIRA *et al.*, 2009), from the southern region of Santa Catarina Island (27°35′ S) to the Cape Santa Marta (28°37′ S) (ACHA *et al.*, 2004; ANDERSON *et al.*, 2015). During austral winters, this area is influenced by the La Plata river plume, which increases nutrients, and the Sub-Antarctic currents, which reduce the temperatures (PIOLA *et al.*, 2000; PIOLA *et al.*, 2005).

The southwestern Atlantic biogeographic ecocline described above is also known as the “Arc of Capricorn”, representing the southernmost limit of distribution of many tropical organisms (ANDERSON *et al.*, 2015; ANDERSON, 2017), a warm temperate biogeographic province (HORTA *et al.*, 2001) or general perspective (SPALDING, MARK D. *et al.*, 2007). This region presents a clear seasonal pattern with lowest surface temperatures around 16 °C observed during winter, and the highest temperatures up to 28 °C observed during summer (ANDERSON *et al.*, 2015; PIRES GOUVÊA *et al.*, 2017). However, a more stable colder condition is observed in its deeper areas as a consequence of the more frequent influence of the SACW (FREIRE *et al.*, 2017).

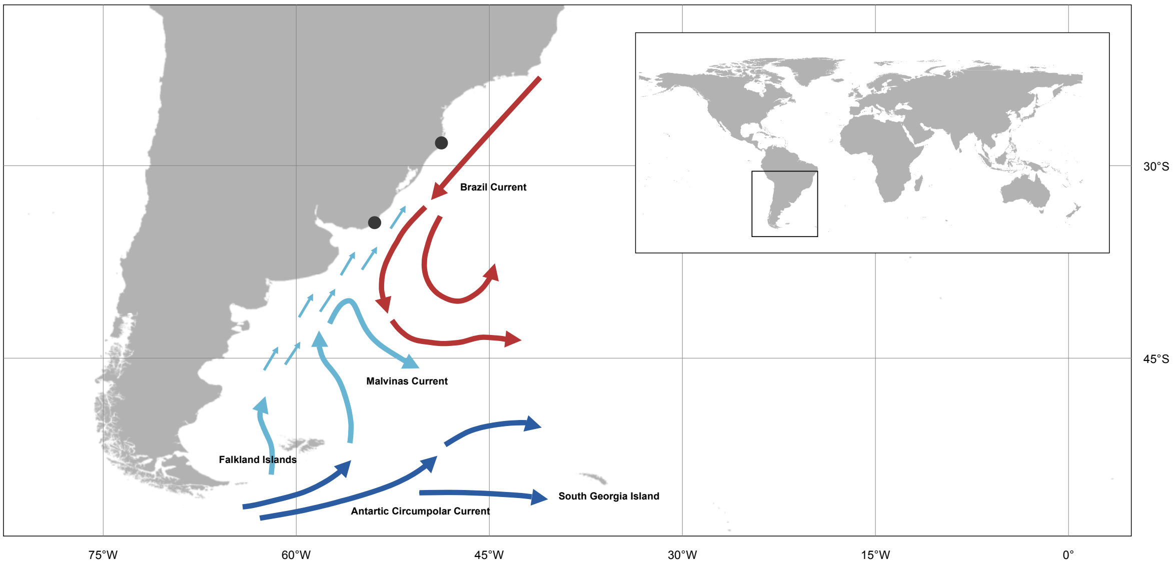

Figure 1. Sampling sites (black points) and main marine currents observed in the drifting region.

2.2. Collection and Characterization

The rafted kelp individuals of *Macrocystis pyrifera* and *Durvillaea antarctica* were collected on the Uruguayan site between 22 July and 3 August and on the Brazilian site between 26 and 29 September 2016, washed-up on the sand strip and drifting in the region of burst. All the individuals were collected and stored in thermal boxes for transport to the Laboratory of Phycology (Federal University of Santa Catarina, Florianópolis, Santa Catarina, Brazil); due to the massive wash-ups on the Uruguayan coast, only some specimens were collected for transport to the Centro Universitario Regional del Este (CURE, UdelaR, Rocha, Uruguay).

To analyze the physiological conditions, of the washed-up specimens, optimum quantum yield was evaluated in three random benthic *Macrocystis* specimens. These specimens were from Punta Arenas, Chile (from different periods, to represent periods of before and after the dispersion event), and they were compared to washed-up plants that were collected in Brazil. Thalli were dark acclimated for 15 min using leaf clips (Diving-LC, Walz) that were placed ~10 cm from the base of each blade, following procedures applied by Edwards and Kim (2010) with North American populations. Maximum (Fm) and the minimum (Fo) fluorescence, and the PSII optimum quantum yield (Fv/Fm) were determined for all three specimens. Relative electron transport rates (rETRs) were calculated as rETR = **Φ** PSII × PPFD; where **Φ** PSII is the quantum efficiency of PSII and PPFD is the photosynthetic photon flux density of photosynthetically active radiation (PAR). Rapid light curves (RLCs) were generated using Walz pre-installed routine. Evaluation of **α**, Ek and rETRmax, (where

α = photosynthetic efficiency under non-saturating irradiances, Ek = saturation irradiance, and rETRmax = the relative maximum rate of electron transfer to photosystem II under saturation irradiances) was accomplished using Platt et al., (1980) equation. RLCs were not evaluated in the Chilean populations.

Samples of *M. pyrifera* were identified based on its external morphology (MACAYA e ZUCCARELLO, 2010), while for *D. antarctica* transverse sections were cut to identify it anatomically (FRASER *et al.*, 2009) (Appendix A). To evaluate the presence of reproductive structures, all morphoanatomical characters, as described by (LEAL *et al.*, 2014), were considered. Fragments from each individual were collected, cleaned and stored in silica gel, for future molecular analyses. Specimens were deposited at the Herbarium FLOR, Federal University of Santa Catarina, Brazil (FLOR 63005, FLOR 63006, FLOR 63007, FLOR 63008, FLOR 63009 and FLOR 630010).

2.3. Niche Modeling Procedures

Macroecological niches of *M. pyrifera* and *D. antarctica* were modeled globally using MaxEnt, a robust method, to predict species distributions with presence-only data (ELITH *et al.*, 2006). This uses the principle of maximum entropy (PHILIPS e DUDÍK, 2008), that compares the occurrence records with pseudo-absences generated from background locations, i.e., possible occurrence areas where the presence/absence of species is unknown (MEROW *et al.*, 2013). The algorithm used in the program was extensively tested in several previous studies (HERNANDEZ *et al.*, 2006; PHILIPS e DUDÍK, 2008; ELITH e LEATHWICK, 2009) and proved to be a reliable tool to be applied in this context. This method provides a suitable technique, as only data collected from the literature is applied to feed the model (VERBRUGGEN *et al.*, 2009b).

2.4. Environmental Variables and Occurrence Data

The environmental variables used to generate niche models were downloaded from Bio-Oracle (TYBERGHEIN *et al.*, 2012a) for the global ocean, under the Behrmann equal-area projection. The selection of variables considered the biology and ecology of kelp forest species (e.g., (ASSIS, J. *et al.*, 2016; ASSIS *et al.*, 2017)), as well as their degree of collinearity inferred with Variance Inflation Factor (VIF) (O'BRIEN, 2007). Environmental variables with VIF scores above 10 were not considered for modelling purposes (O'BRIEN, 2007). This procedure resulted in 9 variables used as input for models.

Georeferenced occurrence data for the whole distribution of species were compiled from the Australian Virtual Database, Global Biodiversity Information Facility (GBIF, www.gbif.org, accessed on 10 December 2016), and scientific journal articles (Table A1). These data were gridded to the spatial resolution of environmental data, and surplus overlapped entries were discarded to eliminate replication. To further reduce the effect of spatial autocorrelation in the models (see (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 1 × 10^4 permutations (e.g., (FERREIRA *et al.*, 2004)). The records were trimmed by randomly selecting one record only, within the radius of the minimum non-significant ($\alpha = 0.05$) spatially correlated distance. This resulted in 224 records for *M. pyrifera* and 112 for *D. antarctica* as input for the models (from a total of 889 records originally compiled for *M. pyrifera* and 616 for *D. Antarctica*) (Table S1).

To reduce estimation bias introduced by the likely unbalanced distribution of data, background information (i.e., "pseudo-absences") were randomly selected per species from a kernel density estimation surface developed with the occurrence records and a spatial grid conformal in resolution with the environmental data (e.g., (BELLWOOD *et al.*, 2004; CHAVES *et al.*, 2013; ASSIS *et al.*, 2017)). This procedure also restricted the extent of models to the actual distribution of species, a crucial step while modelling ecological niches (THRESHER e BROTHERS, 1985; ASSIS *et al.*, 2017).

Over-fitting was controlled by tuning the optimal parameters of models from a range of MaxEnt regularization multipliers (from 0.5 to 5; 0.5 step) and feature classes (i.e., linear, quadratic, hinge, product and threshold) (see (OSÓRIO *et al.*, 2006) for details). A cross-validation framework was implemented in this process to evaluate the performance of models. Statistically independent datasets were produced by partitioning the occurrence records (both presences and pseudo-absences) into 10 distinct latitudinal bands (KRAJEWSKI e FLOETER, 2011). Models testing different parameters interactively fitted data with one band withheld at a time, where performance was evaluated with the area under the curve (AUC) (ALLOUCHE *et al.*, 2006; VERBRUGGEN *et al.*, 2009b) and sensitivity (true positive rate; (BELL, 1983)). Final maps were developed with the combination of parameters retrieving higher average AUC values (identified in cross-validation). These were reclassified to represent suitable/unsuitable areas with the minimum training presence threshold (LEIBOLD *et al.*, 2004; OSÓRIO *et al.*, 2006). All niche modelling analyses were performed with R (R Development Core Team, 2017) using the packages dismo, ecospat, parallel, raster and SDMTool.

2.5. Oceanographic Characterization before and during Dispersion Event

The Southwest Atlantic surface temperature data, before and during the dispersion event, were obtained from the NOAA database. To evaluate the influence of a specific extreme climate episode on the flux of cold water masses from the South Atlantic towards North, we verified the sea surface temperature (SST) from 1 January to 10 October 2016. To exclude the possibility of annual recurrence of the phenomenon, we also verified the flux of water masses during the same period for 2013, 2014 and 2015. SST-anomalies between 2013 and 2016 were evaluated (https://coralreefwatch.noaa.gov/satellite/bleaching5km/index.php). The Group for High-Resolution Sea Surface Temperature (GHRSST) global Level 4 data was obtained from the Physical Oceanography Distributed Active Archive Center (PODAAC), at the NOAA National Centers for Environmental Information, by the satellite AVHRR-ONLY (AVHRR-OI).

3 RESULTS

Entire plants of *M. pyrifera* and *D. antarctica* were collected at La Paloma, Punta del Diablo, Santa Teresa, La Coronilla and Barra del Chuy, east of Uruguay, on 3 August and successive days. A total of 4 m^3 of *M. pyrifera* and 1.3 m^3 of *D. antarctica* were collected from a 2.3 km stretch of beach at Corumbá beach in La Paloma. During the following month, fragments of both species were collected on Campeche beach, along the eastern portion of Santa Catarina Island, southern Brazil. Algae reached Campeche beach on four consecutive days. We collected a total of 1158 g of *M. pyrifera* and 3083 g of *D. antarctica,* their largest recorded sizes were 180 cm and 151 cm, respectively (Figure A1). The *M. pyrifera* rafts that washed-up in Brazil had similar optimum quantum yield variability as compared to plants from natural populations from Chile and North America (Table 1). Reproductive structures were only present in *M. pyrifera* plants from the Uruguayan rafts but absent in both species from the Brazilian rafts.

Table 1 – Comparison of the fluorescence parameters from samples of *M. pyrifera* from the Brazilian rafts, natural populations from the Chilean plants and from natural populations from the North American plants (* = Edwards & Kim 2010; where: Alpha = photosynthetic efficiency; EK = saturated irradiance; rETRmax = relative maximum electron transport rates; and Fv/Fm = maximum quantum yield).

Samples	Alpha	EK	rETRmax	Fv/Fm
Rafts	**0.183 –0.302**	**212.54 –304.00**	**50.16 –88.07**	**0.559 –0.661**
Chilean population/January	**-**	**-**	**-**	**0.584 –0.611**
Chilean population/July	**-**	**-**	**-**	**0.711 –0.722**
Chilean population/August	**-**	**-**	**-**	**0.656 –0.681**
American Population *	**0.3 –0.926**	**34.4 –178.5**	**14.7 –147.4**	**0.4 – 0.75**

Figure 2 shows four sea surface temperature (SST) maps, one per year, and an intrusion of colder waters flowing along the Patagonia shelf, following the Malvinas current (MC) towards the southern coast of Brazil. The lower temperatures recorded were approximately 15 °C in 2013, 2014 and 2015. However, for the same period in 2016, these water masses were colder than compared to 2013, 2014 and 2015, and reached lower latitudes closer to the coast. Figure 2 characterizes a strong advection of cold waters (8–12 °C) from the MC along the Uruguayan and Brazilian shelves. The SST-Anomaly evaluation corroborates previous analyses in the sense that they show a significant inter-annual variability of this cold intrusion.

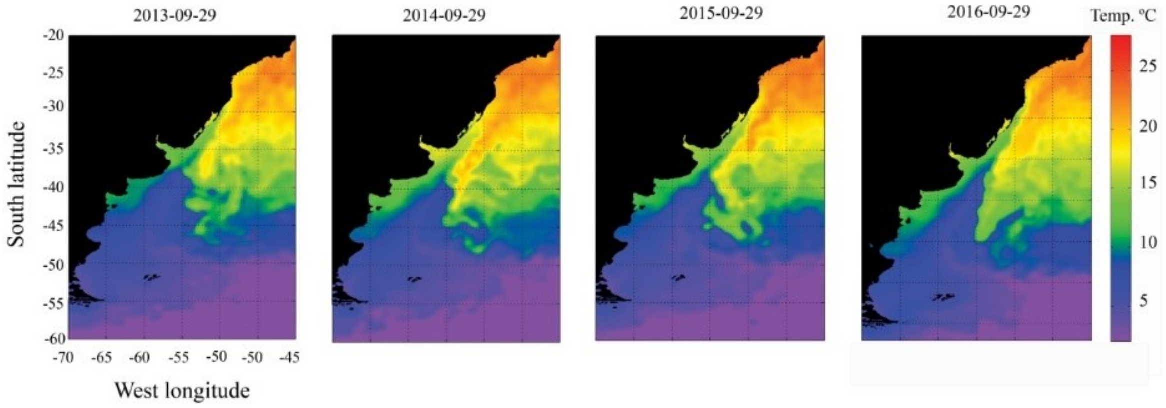

Figure 2 – Sea surface temperature (SST) images for locations between 60° S to 20° S and 45° W to 70° W (29 September) for the years 2013, 2014, 2015 and 2016. The colors indicate differences in SST (°C).

The SST anomaly, with respect to the long-term mean, is presented in Figure 3. In the four maps, warm colors are predominant and this is an indication of the warming of the surface waters of the region. The thermal anomaly along the southernmost third of the South American continental shelf reached 4 °C in 2016. The cold incursion reaches as far north as the southern tip of the South Brazil Bight (SC, Brazil). Animation of daily maps similar to those in Figure 2 clearly shows the northward evolution of the plume. The continuity of the cold anomaly along the coast shown in Figure 3 for 2016-09 suggests northward advection of MC waters- and its contents.

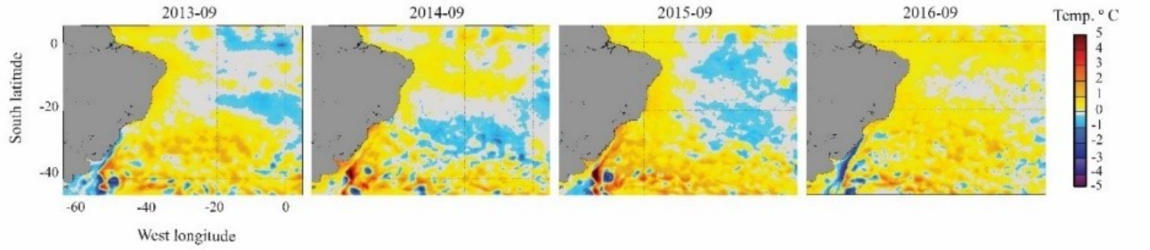

Figure 3 – SST anomaly means (°C) images of locations between 40° S to 0° S and 60° W to 0° W, September, 2013, 2014, 2015 and 2016.

3.1 Niche Models at the Global Scale

The niche models developed for *M. pyrifera* and *D. Antarctica* presented a near-perfect prediction, with mean AUC and mean sensitivity scores inferred in cross-validation >0.9 and >0.95, respectively. The predicted niche suitability in the Southwestern Atlantic Ocean was broader than the known distribution for both species, where the nearest known occurrence distant hundreds of kilometers from the predicted range margin (Figure 4). Among the environmental predictors analyzed, primary productivity (PP), temperatures and phosphates presented the highest contribution to the performance of model for both species. Bottom light also showed to be important restricting vertical distributions, and for *M. pyrifera*, ice thickness (Figure 5).

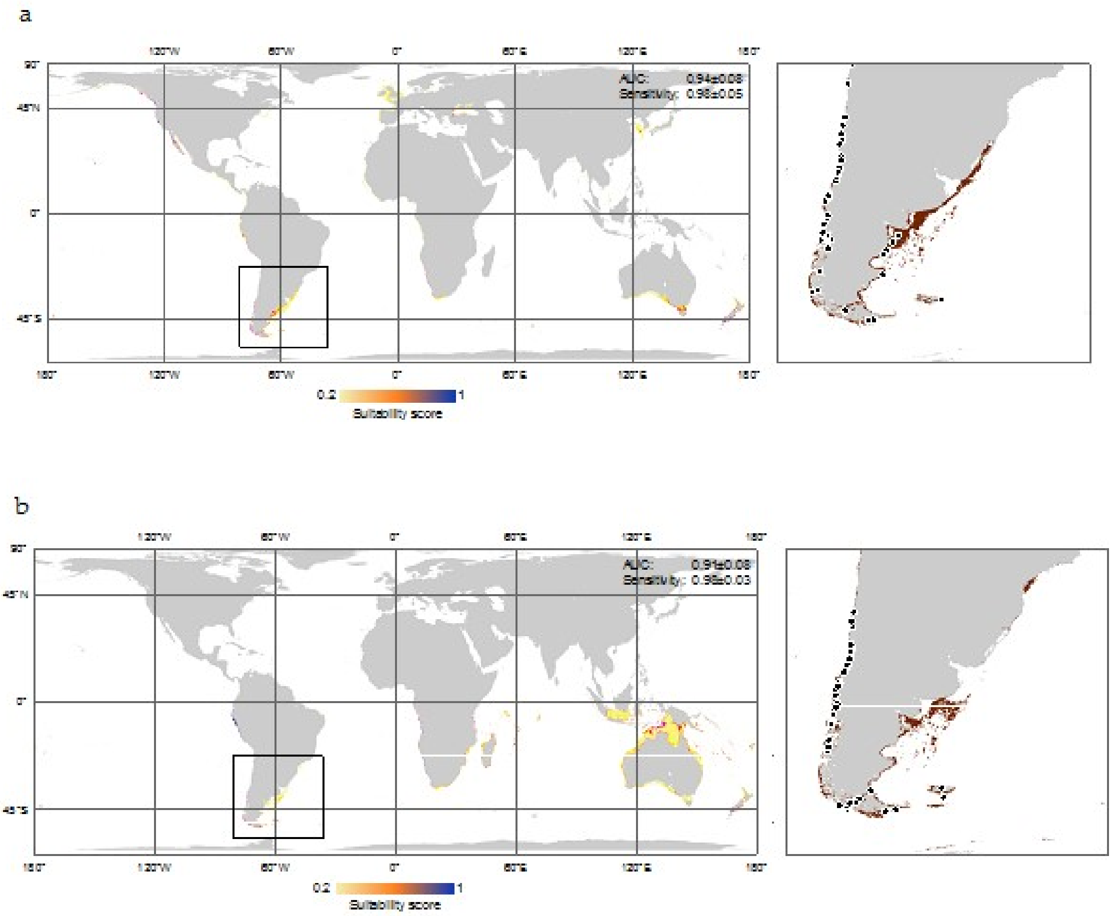

Figure 4. Niche suitability of *Macrocystis pyrifera* (**a**) and *Durvillaea antarctica* (**b**) predicted in Global coastal areas (left) and with highlight to the Southwestern Atlantic Ocean (high) with maximum entropy (models run globally but predicted to the study region). Points depict known records of occurrence. Mean area under the curve (AUC) and mean sensitivity inferred in cross-validation also shown.

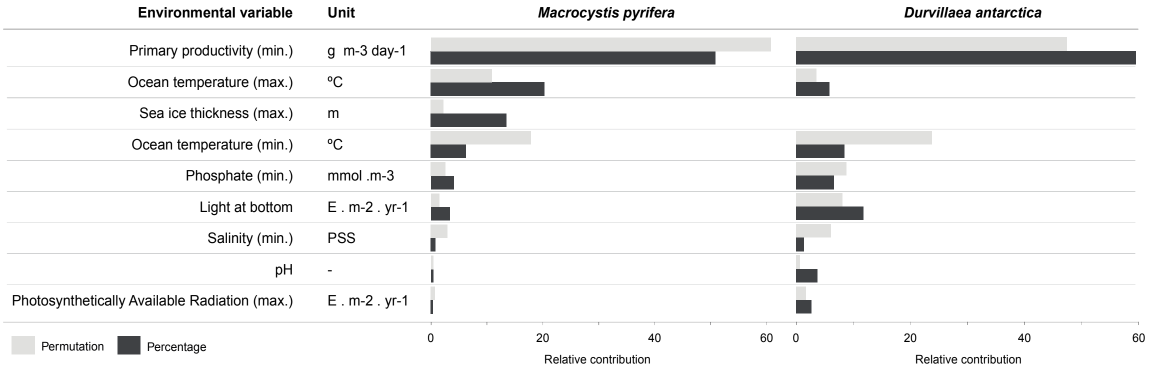

Figure 5. Relative contributions of the environmental variables to the models developed for *Macrocystis pyrifera* and *Durvillaea antarctica*, as percentage contribution and permutation importance.

4 DISCUSSION

The arrival of *M. pyrifera* and *D. antarctica* on the Uruguay and southwestern coast of Brazil represented an intriguing phenomenon that has impressed researchers in physiology and even algae experts around the world (B.M.B. personal communication). The potential origin of these kelp rafts is more than 2000 km away, because the most likely and nearest well-documented occurrence, of both species, is the Falkland Islands (FRASER *et al.*, 2010). The washed up plants, observed on the Uruguayan and Brazilian coasts showed that they have the physiological tools to acclimatize to the floating conditions in this area, during this period (TALA *et al.*, 2016). Despite a long drift process, the oceanographic and climatic conditions (cold water and reduced winter irradiance), observed during the end of the 2016 winter, could be responsible for the good physiological health of the *M. pyrifera* and *D. antarctica* rafts that washed up in Brazil (COYER *et al.*, 2001). Mature sporophylls from the *Macrocystis* rafts that washed up in Uruguay revealed the mechanism that promote connectivity among populations in the Southern Hemisphere and represent a source for colonization of the mapped suitable niches. The niche suitability, which was detected in all the regions that are subject to the Antarctic Circumpolar current, corroborated statements that indicated high connectivity among southern populations. Suitable temperature, irradiance and nutrient conditions, especially during the summer, enabled long-distance dispersion at this latitudinal range, as was hypothesized by Tala et al. [87] and reinforced here by our modeling evaluation.

It is essential to recognize that these species are known for their ability to travel long distances due to morphological structures, such as aerocysts, which provide buoyancy (VAN DEN HOEK e DONZE, 1967; SMITH, 2002; MACAYA *et al.*, 2005; GRIFFITHS e WALLER, 2016). Studies involving passive dispersion of these species recorded distances of tens of kilometers (HERNÁNDEZ-CARMONA *et al.*, 2006; GARDEN *et al.*, 2014). Our data indicate that *M. pyrifera* and *D. antarctica* potentially traveled a distance of at least 2700 km, reaching the Brazilian coast, still alive. Such evidence confirms that *Macrocystis* can grow and keep its reproductive viability while drifting for long periods at latitudes around 27° S during winter (TALA *et al.*, 2016). This high immigration capacity was shown by our physiological data, which demonstrated that raft chlorophyll a fluorescence descriptors were similar to the sessile Chilean and North American populations (EDWARDS e KIM, 2010). An experiment by Hernández-Carmona et al. (HERNÁNDEZ-CARMONA *et al.*, 2006) showed *M. pyrifera* still had viable zoospores after being adrift for 125 days and drifting for a distance of 890 km. This ability is sufficient to connect populations throughout a hemisphere, on a generational time scale, and may even facilitate gene flow between hemispheres under specific meteo-oceanographic conditions.

The floating specimens were found along the Brazilian coast during the last week of September 2016 (late Austral winter), approximately 13 days after the registration of a polar mesocyclone that reached the Argentinean, Uruguayan and Southern Brazilian coasts (Figure 6). Winds of up to 130 km/h were recorded in the coastal region of these countries and a sea level variation of up to 8 m high was recorded in Mar del Plata, Argentina (NOAA 2016). Considering the magnitude of this event and the relationship between extreme events and erosion of kelp forest structure, it is plausible that this storm produced the rafts and promoted the dispersal event. Storms and strong-wind events, such as extratropical cyclones, can detach canopy-forming kelps, transporting the rafts and immigrants, facilitating long-distance dispersal and transport of their propagules to suitable niches (DAYTON e TEGNER, 1984). Furthermore, these storm and strong wind conditions can provide a pick-up/drop off process, and enhance the along-shelf current towards lower latitudes. This period of ideal conditions, with low temperatures and an enhanced northward current is observed at the end of Winter and late Spring in this region (TOKINAGA *et al.*, 2005; CATALDI *et al.*, 2010).

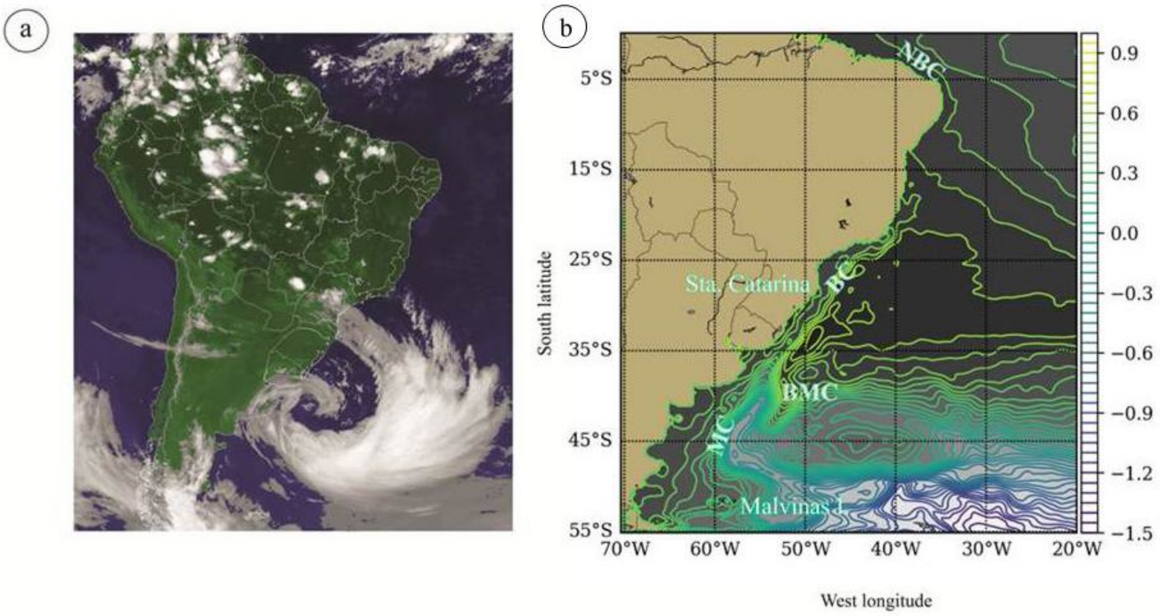

Figure 6 – (**a**) Images of the cyclone recorded on 13 September 2016, captured by the satellite GOES-16 (NOAA); (**b**) Confluence region (BMC) the Brazil (BC) - Malvinas Currents (MC) (Falklands). The colored lines are dynamic temporal mean of the dynamic height, taken between 1993 and 2013. They represent the major geostrophic current systems such as the BC, MC and NBC (North Brazilian Current). In this sense, currents flow parallel to the contours, with higher contours (yellow) on the left height. The intensity of the current is inversely proportional to the spacing between lines. (MDT_CNES-CLS13 was produced by CLS Space Oceanography Division and distributed by Aviso, with support from Cnes (http://www.aviso.altimetry.fr/).

The CBM has an annual latitudinal dynamic, oscillating to the north during the Austral summer and to the south during the Austral winter (OLSON e RICHARDS, 1988). Such variations can be attributed to the large scale variability in the atmospheric forcing, mostly winds of the southern quadrant originating from the Austral Winter (OLSON e RICHARDS, 1988). There is an intensification of the Malvinas Current (CM), which carries Sub Antarctic waters and brings energy to smaller latitudes of the Southern Atlantic (DE SOUZA *et al.*, 2006). Such patterns can be verified in the SST satellite images of 2013, 2014 and 2015, the three years preceding the event (Figure 2). Therefore, the intrusion of cold waters on the southwestern coast of Brazil can be considered a common phenomenon during the Austral winter. However, in 2016, SST maps (Figure 2) showed that, in addition to this cold-water intrusion, that reached lower latitudes, there were intrusions of approximately 8 °C as well as one of approximately 12 °C. During the same period, and in the same region, surface temperature anomalies were captured by the GOES-16 satellite (Figure 3).

Considering the floating and rafting nature of these species, they probably reached the coast of Brazil driven by strong extratropical cyclone winds, and changes in the velocity and SST on the surface coastal currents (PETERSON e STRAMMA, 1991). Moreover, the plume of the La Plata River (35°58′ S; 55°18′ W) along with the south-northward coastal circulation, may have contributed to the dispersal of the individuals of *D. antarctica* and *M. pyrifera* to the coastal region of southwestern Brazil. Nutrient enrichment from rivers and upwelling feed the high demand of kelp species for nitrogen and phosphate (COYER *et al.*, 2001), helping in the resilience of rafts during the long drift.

The destination of floating algae, in medium and lower latitudes, is mainly determined by the combination of abiotic and biotic factors (e.g., temperature currents, irradiation, and suitable habitats) (CLENDENNING, 1971; MACAYA *et al.*, 2005; ROTHÄUSLER *et al.*, 2011). Rothäusler et al., (2011) showed that floating *Macrocystis*, at mid-latitudes, (25° S–40° S) have a higher physiological adaptability and consequent ability to float for long periods of time, and over long distances, surviving at temperatures ranging between 12 °C and 20 °C (MACAYA *et al.*, 2005). Experimentally they also showed that *M. pyrifera* could not withstand temperatures higher than 24 °C, and specimens perished after 5 days. Nevertheless, in northern Baja California *M. pyrifera* populations are exposed to SST variations of between 12.7 °C to 22.5 °C, while the southernmost subtropical populations show warmer temperature tolerances varying between 15.6 °C to 25.5 °C (COLOMBO-PALLOTTA *et al.*, 2006). It is already well established that climate changes can affect substantially species distribution and, more particularly, alter the rafts' trajectory, which will influence the dispersal and distribution of marine organisms (HERNÁNDEZ-CARMONA *et al.*, 2006; CHEUNG *et al.*, 2009; GARDEN *et al.*, 2014). Therefore, this aspect should be considered with particular attention.

Along the Brazilian coast, the algae were washed up at the beach and drifted in the breakwater zone, which does not allow one to confirm whether these species inhabited the region. However, the near-perfect prediction, indicating that at the spatial scale of our study, the environmental variables used, explained the actual species distributions, and pose the discussion regarding distribution extension (VERBRUGGEN *et al.*, 2009b). The main predictors which influenced the models were variables related to PP, temperature and, nutrient availability and light. Due to the physiological requirements and affinities of the species known for low temperatures (MACAYA *et al.*, 2005), we can confirm that *maximum SST* and *bottom light* were the limiting factors for latitudinal and vertical distribution. Such a conclusion is evident when we observe the georeferenced distribution of species restricted to environments in high and medium latitudes in shallow areas, where the temperature and radiation were lower. The partial dependency function shows that primary PP limits the distribution of *Macrocystis* and *Durvillaea* on its very low levels, commonly observed in lower latitudes and deeper ocean regions. PP combines in a single predictor the resource availability, involving irradiance, CO2, temperatures and nutrients (REED *et al.*, 2016). This shows the negative effect of oligotrophic regions and positive effect that upwelling and medium latitudes regions have globally (e.g., (REED *et al.*, 2016)). The model (Figures 4 5) reinforces the sensitivity of these species to changes in temperature, radiation and water quality (i.e., especially turbidity), because these are the factors that delimit their geographical distribution (DAYTON, 1985; GRAHAM *et al.*, 2007). However, it points towards probable refuge regions, interestingly, in lower latitudes, far from regions previously recognized with "optimum" environmental conditions, extrapolating their suitable habitats also to other temperate regions in the Northern Hemisphere. The regional cooling of coastal environments observed in the southwestern Atlantic warm temperate province southern edge (FALVEY e GARREAUD, 2009; PEREIRA *et al.*, 2009) corroborate the niche suitability described for the south of Brazil and Uruguay. The range extension of the South African kelp, *Ecklonia maxima*, was also ascribed to a regional cooling process (BOLTON *et al.*, 2012). Therefore, kelps are ecosystem engineers, responsible for most of the primary production where they occur. This would mean that the spread or dispersal of kelps could have ecological, economical and sociological consequences.

In addition, it is likely that the ideal habitats for these species are located at deeper strata of the region. Studies report that some kelp species move to deeper water in a response to warming trends (LADAH LYDIA e ZERTUCHE-GONZÁLEZ JOSÉ, 2004; PEHLKE e BARTSCH, 2008; ASSIS, V. D. L. *et al.*, 2016). Species occurring in the tropics with high temperate affinities tend to occupy deeper niches (GRAHAM *et al.*, 2007), as is the case of *Laminaria abyssalis*, the only kelp-forming species ever recorded on the Brazilian coast (MARINS *et al.*, 2014). *Laminaria abyssalis* is endemic to the Brazilian coast and has a specific biotope. It occurs on rhodolith beds (21° S and 40° W) at depths between 40 to 120 m, at temperatures of between 15–19 °C, and at low light intensity (YONESHIGUE-VALENTIN, 1990; YONESHIGUE-VALENTIN *et al.*, 1995). Due to the influence of SACW, deeper waters in southern Brazil are colder and is less variable when compared to surface (FREIRE *et al.*, 2017) conditions, most of the time, optimal or tolerated for both kelp species.

Therefore, it is important to note that environmental variables used in the model are collected from the ocean surface. Considering deeper environments in the continental platform, it would be reasonable to assume that the probability of finding suitable habitats for these species would be even greater. Many suitable deeper refuges for these species can be identified, such as the Rio Grande rocky parcels at Rio Grande Sul State, southern Brazil, or Vitória Trindade seamounts, Espírito Santo State, southwestern Brazil. In these environments the topography of the seamounts can promote the upwelling of the cold nutrient rich waters, cooling and fertilizing the warmer, oligotrophic shallow waters (O'HARA *et al.*, 2010), and in turn provide potentially ecophysiological conditions for the development of kelp spores or germlings (COYER *et al.*, 2001). We reinforce that the apparent absence of both species in areas with high habitat suitability is probably a consequence of absence or scarcity of sampling efforts. Therefore, suitability maps can be utilized in the definition of target areas for further surveys regarding kelp presence and kelp forest composition, diversity and connectivity.

However, populations of *M. pyrifera* may be limited not only by physical factors such as temperature, light and nutrients, but also by the type of substrate and the presence of herbivores (e.g., sea urchin species such as *Loxechinus albus*) (DAYTON, 1985). Due to a lack of available herbivore data, on a global scale, among other important biological interactions, these biotic factors were not considered in our evaluations.

The introduction of benthic macroalgae is a frequent phenomenon in coastal regions (WILLIAMS e SMITH, 2007; RAFFO *et al.*, 2009). Recently, the occurrence of *Grateloupia turuturu* Yamada was documented in the south-western Atlantic, more specifically on the coast of the state of Santa Catarina, in Brazil (AZEVEDO, CASSANO, JÚNIOR, BATISTA e OLIVEIRA, 2015). Despite its high potential as an invasive algae species in the world, *G. turuturu* has a higher affinity for temperate environments (AZEVEDO, CASSANO, JÚNIOR, BATISTA e OLIVEIRA, 2015). The species, which was first detected in the Southwestern Atlantic in 2011, can easily be found on the rocky shores near the point where the washed-up kelp rafts were found.

The effects of the arrival of kelp species such as *M. pyrifera* and *D. antarctica* in a new ern pacific populations have varied, over hundreds of kilometers along the Baja Califunexpected environment is still not documented, although the southern limit of the northeastornia peninsula, during the past 20 years (EDWARDS e HERNANDEZ-CARMONA, 2005). Migration is a fundamental process to increase resilience of populations, a natural part of an eco-evolutionary framework (FACON *et al.*, 2006), where selective pressure variability meet phenotypic plasticity of the respective immigrant population. Therefore, if they are part of a natural dynamic equilibrium of marine environments these events should be better understood and preserved. Alternatively, if anthropogenic vectors promote it, these events must be evaluated under the usual bioinvasion perspective, and the management of this process should consider eradication. The kelp *Undaria pinnatifida*, also a canopy-forming kelp, is rated as the fifth most successful invasive species in the world (NYBERG e WALLENTINUS, 2005; RAFFO *et al.*, 2009). However, studies have shown that where *U. pinnatifida* invaded there was no evidence of interspecific competition, except for small effects on the abundance of some species of intertidal communities (RAFFO *et al.*, 2009; SOUTH *et al.*, 2015). Therefore, healthy forests of fucoids tend to resist invasions, unless the canopy is disturbed (VALENTINE e JOHNSON, 2003; THOMPSON e SCHIEL, 2012). So far, there are no records on the effects of kelp-forming algae invading regions where no large algae forests occur.

The niche model results reinforce the need for transnational discussions regarding habitats, considered refuges for conservation initiatives in a global context of climate change intensification (BERNHARDT e LESLIE, 2013; CHALLINOR *et al.*, 2017). Such an environmental change could produce meteo-oceanographic events which could displace large amount of kelp rafts over long distances. In addition to these events, ocean acidification could cause disturbances in underwater autochthone communities, producing opportunities for kelp immigration that could change the resilience of eventual host communities (BARRY *et al.*, 1995). Considering the importance of these organisms to coastal ecology (e.g., carbon fixation from the atmosphere, increasing habitat complexity and diversity) (WHEELER, 1980; GRAHAM *et al.*, 2007), these questions should be discussed at international forums and monitoring programs should be planned to consider possible origins and dispersal routes. These discussions should influence planning and the design, size and position of marine protected areas (MPA) that should add as potential services the preservation of species with this ability to survive long periods drifting.

5. CONCLUSIONS

The occurrence of these kelp rafts in the Brazilian and Uruguayan coast does not characterize the expansion of their limits of occurrence because settled populations were not found. However, such events could be regarded as an indication of change in climatic/oceanographic processes. Our results indicate that viable rafts can travel long distances, which demand a further discussion about long-term management of these immigration events. Therefore, changes in current temperatures and patterns may alter kelps raft routes and potential colonization areas. Considering the remarkable role that these rafts play in facilitating the dispersal and connectivity between coastal faunal and floristic communities, events such as this require greater attention regarding invasive species monitoring programs, niche conservation policies and climatic changes.

Supplementary Materials: The following are available online at www.mdpi.com/link, Table S1: Georeferenced Occurrences *Macrocystis pyrifera* and *Durvillaea antartica* used to generate the model and video S1: Images of sea surface temperature (SST) for locations between 60 ° S at 20 ° S and 45 ° W at 70 ° W between the months of January and September 2016.

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Author Contributions: conceived and wrote the paper: M.B.B. and P.A.H.; detected and collected species: A.B.A., G.V.-R., F.S., A.M., L.O., G.F.; extracted data from Web of Science: C.S., J.A. and M.B.B.; analyzed the data: P.F.S, P.S.P., T.C.L.S.,

A.A.B. and M.B.B; contributed with data: G.L., J.O., A.M.; critical revision and discussions: P.A.H., O.C., M.D.R., L.B., J.A., E.A.S. and R.S.

Conflicts of Interest: The authors declare no conflict of interest.

APPENDIX

Figure A1 – *Macrocystis pyrifera* (**A**, **B**, **C**) and *Durvillaea antarctica* (**D**) on the Uruguayan beach and their respectives fragments (**E** and **F**) that arrived in south of Brazil collected at Campeche Beach, south of Brazil (scales: C = 15 cm; D = 30 cm, E = 10 cm, F = 10 cm).

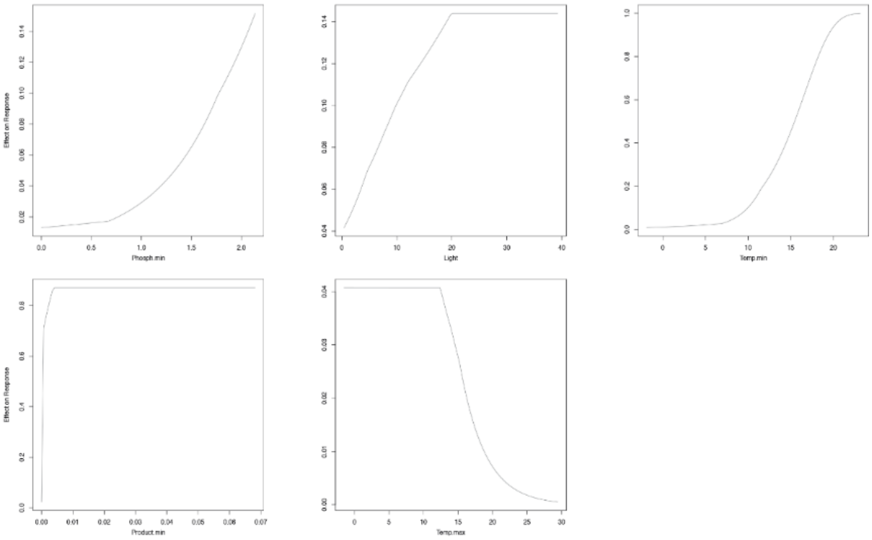

Figure A2 – *Durvillaea antarctica* parcial plots.

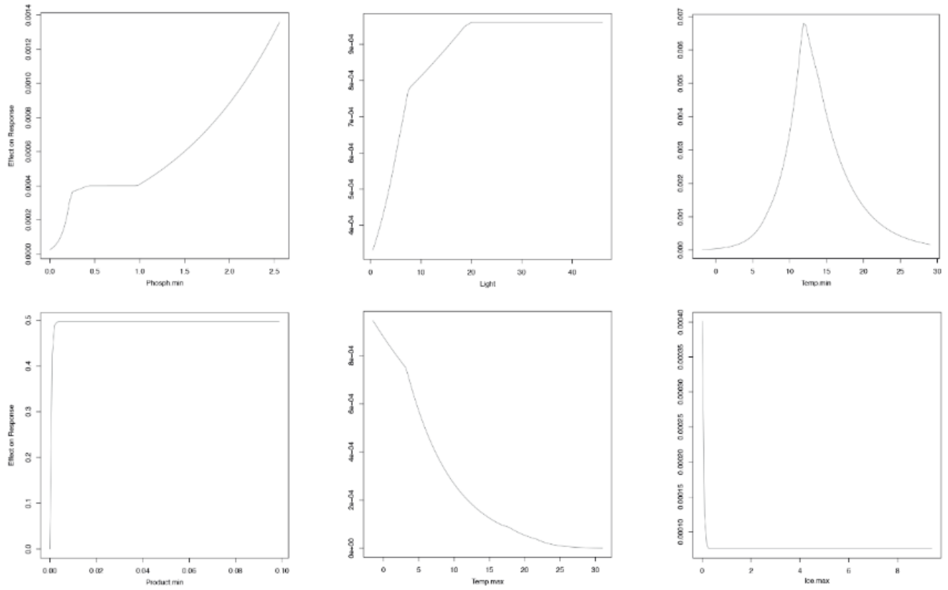

Figure A3 – *Macrocystis pyrifera* parcial plot

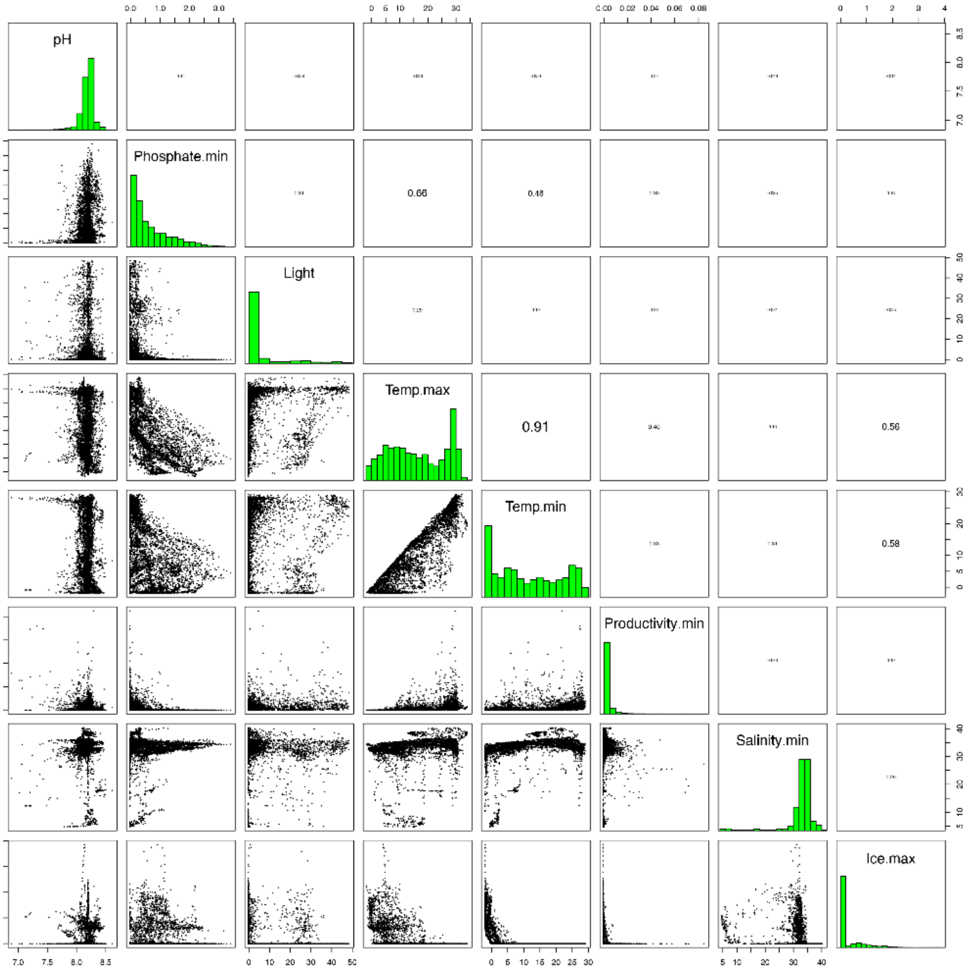

Figure A4. Pairs plots.

Table A1. Scientific articles used to obtain records of occurrence of the species *Macrocystis pyrifera* (**A**) and *Durvillaea antarctica* (**B**).

Species	Citation
A	Barrales, H.L.; Lobban, C.S. The comparative ecology of *Macrocystis pyrifera*, with emphasis on the forests of Chubut, Argentina. *The Journal of Ecology* 1975, 657-677.
A	Dayton, P. Kelp communities of southern south America. *Antarct J US* 1974.
A	Zimmerman, R.C.; Kremer, J.N. In situ growth and chemical composition of the giant kelp, *Macrocystis pyrifera:* Response to temporal changes in ambient nutrient availability. *Marine Ecology Progress Series* 1986, 277-285.
A	Macaya, E.C.; Zuccarello, G.C. Genetic structure of the giant kelp em *Macrocystis pyrifera* along the southeastern pacific. *Marine Ecology Progress Series* 2010, *420*, 103-112.
A	Beas-Luna, R.; Ladah Lydia, B. Latitudinal, seasonal, and small-scale spatial differences of the giant kelp, *Macrocystis pyrifera*, and an herbivore at their southern range limit in the northern hemisphere. In *Botanica Marina*, 2014; Vol. 57, p 73.
A	Johansson, M.L.; Alberto, F.; Reed, D.C.; Raimondi, P.T.; Coelho, N.C.; Young, M.A.; Drake, P.T.; Edwards, C.A.; Cavanaugh, K.; Assis, J. Seascape drivers of *Macrocystis pyrifera* population genetic structure in the northeast pacific. *Molecular ecology* 2015, *24*, 4866-4885.
A	Riosmena-Rodríguez, R.; Boo, G.H.; López-Vivas, J.M.; Hernández-Velasco, A.; Sáenz-Arroyo, A.; Boo, S.M. The invasive seaweed Sargassum filicinum (Fucales, Phaeophyceae) is on the move along the Mexican pacific coastline. *Botanica Marina* 2012, *55*, 547-551.
A	Starko, S.; Martone, P.T. Evidence of an evolutionary-developmental trade-off between drag avoidance and tolerance strategies in wave-swept intertidal kelps (Laminariales, Phaeophyceae). *Journal of phycology* 2016, *52*, 54-63.
A	Ladah Lydia, B.; Zertuche-González José, A. Giant kelp (*Macrocystis pyrifera*) survival in deep water (25–40 m) during el Niño of 1997–1998 in Baja California, Mexico. In *Botanica Marina*, 2004; Vol. 47, p 367.
A	Asensi, A.O.; Küpper, F.C. Seasonal periodicity and reproduction of brown algae (Phaeophyceae) at Puerto Deseado (Patagonia). *Botanica Marina* 2012, *55*, 217-228.
A	Cazón, J.P.; Viera, M.; Sala, S.; Donati, E. Biochemical characterization of *Macrocystis pyrifera* and *Undaria pinnatifida* (Phaeophyceae) in relation to their potentiality as biosorbents. *Phycologia* 2014, *53*, 100-108.
A	Macaya, E.C.; Boltaña, S.; Hinojosa, I.A.; Macchiavello, J.E.; Valdivia, N.A.; Vásquez, N.R.; Buschmann, A.H.; Vásquez, J.A.; Alonso Vega, J.M.; Thiel, M. Presence of sporophylls in floating kelp rafts of *Macrocystis spp.*

	(Phaeophyceae) along the Chilean pacific coast. *Journal of Phycology* 2005, *41*, 913-922.
A	Engel, C.R.; Billard, M.V., Emmanuelle; Viard, F. Conservation and polymorphism of mitochondrial intergenic sequences in brown algae (Phaeophyceae). *European Journal of Phycology* 2008, *43*, 195-205.
A	Rothäusler, E.; Gómez, I.; Karsten, U.; Tala, F.; Thiel, M. Physiological acclimation of floating *Macrocystis pyrifera* to temperature and irradiance ensures long-term persistence at the sea surface at mid-latitudes. *Journal of Experimental Marine Biology and Ecology* 2011, *405*, 33-41.
A	Van Tussenbroek, B. Plant and frond dynamics of the giant kelp, *Macrocysti spyrifera*, forming a fringing zone in the Falkland Islands. *European Journal of Phycology* 1993, *28*, 161-165.
A	Hurd, C.L.; Pilditch, C.A. Flow-induced morphological variations affect diffusion boundary-layer thickness of *Macrocystis pyrifera* (Heterokontophyta, Laminariales). *Journal of phycology* 2011, *47*, 341-351.
A	Ricker, R.W. *Taxonomy and biogeography of Macquarie Island seaweeds*. British Museum (Natural History): 1987.
A	John, D.M.; Pugh, P.J.; Tittley, I. Observations on the benthic marine algal flora of South Georgia: A floristic and ecological analysis. *Bulletin of the Natural History Museum. Botany series* 1994.
A	Hay, C.H. A new species of *Macrocystis*c. Ag. (Phaeophyta) from Marion Island, Southern Indian ocean. *Phycologia* 1986, *25*, 241-252.
B	Boraso, A.; Zaixso, J. Atlas de sensibilidad ambiental de la costa y el mar argentino. *Algas marinas bentónicas* 2011, 1-28.
B	Boraso, A.L. Elementos para el estudio de las macroalgas de argentina. *Comodoro Rivadavia: Editorial Universitaria de la Patagonia EDUPA* 2013.
B	Graiff, A.; Karsten, U.; Meyer, S.; Pfender, D.; Tala, F.; Thiel, M. Seasonal variation in floating persistence of detached *Durvillaea antarctica* (chamisso) hariot thalli. *Botanica Marina* 2013, *56*, 3-14.
B	López, B.A.; Macaya, E.C.; Tala, F.; Tellier, F.; Thiel, M. The variable routes of rafting: Stranding dynamics of floating bull kelp *Durvillaea antarctica* (Fucales, Phaeophyceae) on beaches in the se pacific. *Journal of phycology* 2017, *53*, 70-84.
B	Cho, G.Y.; Rousseau, F.; De Reviers, B.; Boo, S.M. Phylogenetic relationships within the Fucales (Phaeophyceae) assessed by the photosystem i coding psa a sequences. *Phycologia* 2006, *45*, 512-519.
B	Fraser, C.I.; Hay, C.H.; Spencer, H.G.; Waters, J.M. Genetic and morphological analyses of the southern bull kelp *Durvillaea antarctica* (Phaeophyceae: Durvillaeales) in new Zealand reveal cryptic species. *Journal of Phycology* 2009, *45*, 436-443.
B	Wells, E.; Brewin, P.; Brickle, P. Intertidal and subtidal benthic seaweed diversity of South Georgia. *Norfolk, UK* 2011.

B	Ortiz, J.; Romero, N.; Robert, P.; Araya, J.; Lopez-Hernandez, J.; Bozzo, C.; Navarrete, E.; Osorio, A.; Rios, A. Dietary fiber, amino acid, fatty acid and tocopherol contents of the edible seaweeds *Ulva lactuca* and D*urvillaea antarctica*. *Food chemistry* 2006, *99*, 98-104.
B	Bustamante, R.; Castilla, J. Impact of human exploitation on populations of the intertidal southern bull-kelp *Durvillaea antarctica* (Phaeophyta, Durvilleales) in central Chile. *Biological Conservation* 1990, *52*, 205-220.
B	Smith, S.; Simpson, R. Effects of the'nella dan'oil spill on the fauna of *Durvillaea antarctica* holdfasts. *Marine Ecology Progress Series* 1995, 73-89.
B	Collins, C.J.; Fraser, C.I.; Ashcroft, A.; Waters, J.M. Asymmetric dispersal of southern bull-kelp (*Durvillaea antarctica*) adults in coastal New Zealand: Testing an oceanographic hypothesis. *Molecular Ecology* 2010, *19*, 4572-4580.
B	Smith, J.; Bayliss-Smith, T. Kelp-plucking: Coastal erosion facilitated by bull-kelp *Durvillaea antarctica* at subantarctic Macquarie Island. *Antarctic Science* 1998, *10*, 431-438.
B	Dillehay, T.D.; Ramirez, C.; Pino, M.; Collins, M.B.; Rossen, J.; Pino-Navarro, J. Monte verde: Seaweed, food, medicine, and the peopling of South America. *Science* 2008, *320*, 784-786.
B	Taylor, D.I.; Schiel, D.R. Self-replacement and community modification by the southern bull kelp *Durvillaea antarctica*. *Marine Ecology Progress Series* 2005, *288*, 87-102.
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CONCLUSÃO GERAL

Com base nos resultados apresentados neste trabalho, concluímos que a "alface do mar", pertencente ao gênero *Ulva*, é representada globalmente por diferentes espécies. Esta revisão molecular global realizada no Capítulo 1, que inclui pela primeira vez representantes do Atlântico Sul, mostrou um número considerável de táxons com determinações variadas presentes no mesmo clado, o que salienta a necessidade deste amplo estudo. A partir desta análise filogenética, foi possível observar uma diminuição do número de táxons já descritos morfológicamente, em relação às entidades moleculares infragenéricas. Na costa do Brasil, foi identificado apenas um táxon, o qual denominamos *Ulva fasciata*. É possível que as algas identificadas anteriormente como *Ulva lactuca*, *Ulva fasciata* e *Ulva rigida* na região, sejam todas pertencente a entidade molecular *Ulva fasciata*. No entanto, salientamos a necessidade de sequenciamento e disponibilização das informações moleculares de pelo menos um dos espécimes tipo, para uma conclusão nomenclatural definitiva do grupo. O clado classificado como *Ulva fasciata* apresentou um caráter cosmopolita, com maior diversidade genética em regiões tropicais na costa do Brasil e da Índia. Esse padrão pode ser atribuído a influência de drivers macroecológicos, especialmente representado pela temperatura. A segregação de haplótipos em diferentes regiões biogeográficas (Tropical e Temperada-quente), pode ser um exemplo da influência da temperatura no processo de especiação nestas algas. Ainda no Capítulo 1, detectamos a presença de uma espécie críptica, considerada invasora e considerada oportunista devido a sua propensão a formação de "marés verdes". A identificação desta espécie só foi possível após a análise molecular, o que salienta a importância desta ferramenta como aliada às ações preventivas relacionadas às espécies invasoras e manejo costeiro.

A detecção de jangadas de kelps composta por duas espécies de algas não-nativas nas costas uruguaias e brasileiras, descrita no Capítulo 2, reforça a hipótese de que o Atlântico Sudoeste é uma região propensa a entrada de espécies invasoras. Apesar da presença destas jangadas não caracterizar a expansão dos limites de ocorrência destas espécies, os resultados do modelo de nicho, mostram que esta é uma região de colonização potencial para estas espécies. Tanto a distribuição real destas espécies (*M. pyrifera* e *D. antarctica*), quanto a previsão de nicho adequado, foram fundamentadas a partir da combinação de preditores ambientais tais como a temperatura, disponibilidade de nutrientes e luz. Contudo, este trabalho contribuiu também para o entendimento de vetores atuantes na dispersão de algas, que podem ser mediadas tanto pela ação humana direta como incrustações em cascos de transportes aquáticos quanto por mudança nos processos climáticos / oceanográficos. Por fim, considerando o notável papel ecológico, tanto de jangadas de kelps quanto de espécies chaves do gênero *Ulva*, destacamos a importância da inclusão destes registros em programas de monitoramento de espécies invasivas, políticas de conservação de nicho e mudanças climáticas.