

The floating *Sargassum* (Phaeophyceae) of the South Atlantic Ocean – likely scenarios

MARINA NASRI SISSINI^{1*}, MARIA BEATRIZ BARBOSA DE BARROS BARRETO², MARIA TERESA MENEZES SZÉCHY², MARCOS BOUÇAS DE LUCENA³, MARIANA CABRAL OLIVEIRA⁴, JIM GOWER⁵, GANG LIU^{6,7}, EDUARDO DE OLIVEIRA BASTOS⁸, DANIELA MILSTEIN⁹, FELIPE GUSMÃO⁹, JOSÉ EDUARDO MARTINELLI-FILHO¹⁰, CÍCERO ALVES-LIMA¹¹, PÍO COLEPICOLA¹¹, GABRIEL AMEKA¹², KWEKU DE GRAFT-JOHNSON¹², LIDIANE GOUVEA¹, BEATRIZ TORRANO-SILVA⁴, FÁBIO NAUER⁴, JOSÉ MARCOS DE CASTRO NUNES¹³, JOSÉ BONOMI BARUFI¹⁴, LEONARDO RÖRIG¹⁴, RAFAEL RIOSMENA-RODRÍGUEZ^{15†}, THAYNÁ JEREMIAS MELLO¹⁶, LETICIA VERAS COSTA LOTUFO¹⁷ AND PAULO ANTUNES HORTA¹

¹Programa de Pós-graduação em Ecologia, Universidade Federal de Santa Catarina, Florianópolis, Brazil

²Instituto de Biologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil

³Universidade Federal Fluminense, Rio de Janeiro, Brazil

⁴Instituto de Biociências, Universidade de São Paulo, São Paulo, Brazil

⁵NOAA Center for Weather and Climate Prediction, College Park, MD 20740, USA

⁶Coral Reef Watch, National Oceanic and Atmospheric Administration, College Park, MD 20740, USA

⁷Global Science and Technology, Inc., Greenbelt, MD 20770, USA

⁸Programa de Pós-graduação em Biotecnologia e Biociências, Universidade Federal de Santa Catarina, Florianópolis, Brazil

⁹Universidade Federal de São Paulo, São Paulo, Brazil

¹⁰Instituto de Geociências, Universidade Federal do Pará, Belém, Brazil

¹¹Departamento de Bioquímica, Instituto de Química, Universidade de São Paulo, São Paulo, Brazil

¹²University of Ghana, Legon, Ghana

¹³Universidade Federal da Bahia, Salvador, Brazil

¹⁴Laboratório de Ficologia, Universidade Federal de Santa Catarina, Florianópolis, Brazil

¹⁵Universidad Autonoma de Baja California Sur, Mexicali, Mexico

¹⁶Parque Nacional Marinho de Fernando de Noronha, Instituto Chico Mendes de Conservação da Biodiversidade, Brasília, Brazil

¹⁷Instituto de Ciências Biológicas, Universidade de São Paulo, São Paulo, Brazil

ABSTRACT: This study represents the efforts of a network of researchers to characterise the large, floating *Sargassum* (Fucales, Phaeophyceae) biomass that had reached the Brazilian coast in 2014 and 2015. Material collected during these events was identified as *Sargassum natans* and *S. fluitans* using morphological characteristics; ITS2 sequences showed low divergence (0%–3%) with sequences of nine other *Sargassum* species. Several epiphytic macroalgae, invertebrates and fishes were associated with the floating *Sargassum*. Satellite images did not support the hypothesis of slicks moving south from the Sargasso Sea in the northern Atlantic Ocean. This strengthens the hypothesis that there is a matrix of pelagic *Sargassum* in the central Atlantic Ocean and that biomass accumulation should be considered a result of the combination of physicochemical seawater conditions and biological interactions. The biomass accumulation of the stranded *Sargassum* was estimated during four events, peaking in 98 kg m⁻² wet weight on a beach on the Amazonian coast. The landing of huge *Sargassum* biomass represents a potential source of environmental stress, as it can lead to an increase in oxygen demand and eventually synthesise and release chemical compounds with allelopathic properties. On the other hand, these floating islands are a fundamental element of the biogeography and macroecology of tropical environments in the Atlantic Ocean, providing connectivity south/north and east/west among marine biodiversity from Atlantic reef environments. Studies concerning *Sargassum* effects on local communities are necessary for the proper management of this phenomenon.

KEY WORDS: Dispersal, Golden tide, Pelagic *Sargassum*, Sargasso Sea

INTRODUCTION

Floating *Sargassum* is well known since the 19th century from the Sargasso Sea, a region in the northwestern Atlantic Ocean occupying approximately 4,164,000 km² extending between 22°–38°N and 76°–43°W and centred on 30°N and 60°W. The Sargasso Sea is formed by floating masses of

Sargassum natans (Linnaeus) Gaillon and *S. fluitans* (Børgesen) Børgesen (Butler *et al.* 1983; Guiry & Guiry 2016). The floating *Sargassum* provides substrate, shelter and feeding grounds for invertebrates, turtles and fishes, of which 10 species are endemic (Butler *et al.* 1983; Laffoley *et al.* 2011). Due to their unequivocal evolutionary, ecological and economic importance, conservation initiatives look to protect this particular environment, especially in areas beyond any national jurisdictions (Warner 2014). The establishment of the Sargasso Sea Commission (<http://www.sargassoalliance.org>) encourages and facilitates volun-

* Corresponding author (msissini@gmail.com).

† Deceased.

DOI: 10.2216/16-92.1

© 2017 International Phycological Society

tary collaboration toward the conservation of this environment in regard to its health, productivity and resilience.

The singular condition of the subtropical convergence zone concentrates the main floating *Sargassum* patches from the Gulf of Mexico to the open sea. These floating islands are directed by surrounding currents (Sehein *et al.* 2014) that also transport the *Sargassum* and the associated biota across a broad area and to long distances, influencing and even enhancing the dispersion process of marine organisms that utilise them as rafts (Thiel & Gutow 2005; Luiz *et al.* 2015). However, recent changes in patterns of surface currents may be displacing this drifting environment to new regions, offshore (Széchy *et al.* 2012; Gower *et al.* 2013; Moreira & Alfonso 2013) and to coastal areas (Gavio *et al.* 2015). *Sargassum* masses arriving on the coast may be a threat to coastal environments, as biomass decomposition has negative effects on tourism activities as well as local fisheries (Solarin *et al.* 2014). Furthermore, pelagic *Sargassum* potentially brings rafter and associated species that are exotic to different ecosystems, compromising their equilibrium (Ferreira *et al.* 2009).

Széchy *et al.* (2012) reported the first occurrence of *Sargassum* masses offshore on the northern Brazilian coast in July 2011 (Fig. 1). In the same year, pelagic *Sargassum* reached the coast of western Africa, from Sierra Leone to Ghana (Johnson *et al.* 2013; Smetacek & Zingone 2013), in an unprecedented event named the ‘golden tide’. In April 2015, floating masses of *Sargassum* were observed arriving at Fernando de Noronha Archipelago (03°50’S, 32°25’W), a marine national park 345 km from the northeastern coast of Brazil, coming from the eastern side of the South Atlantic Ocean. Afterwards, an enormous amount of stranded *Sargassum* was recorded in coastal regions of Brazil, including Pará (00°35’S, 47°17’W) and Maranhão (2°29’S, 44°17’W) states. Slicks of *Sargassum* were also spotted next to the Brazilian oceanic islands of Rocas Atoll (03°52’S, 33°48’W) and São Pedro and São Paulo Archipelago (00°55’N, 29°20’W), 230 km and 1000 km from the Brazilian coast, respectively (Fig. 1). We have gathered information on the unusual *Sargassum* biomass reaching the shores of the South Atlantic, attempting to explain its origin, the main environmental drivers and alternatives for management.

MATERIAL AND METHODS

Characterisation of *Sargassum* stranded on the Brazilian shore was provided by a network of researchers. Collected ramets were identified based on their external morphology available descriptions of floating using *Sargassum* (Taylor 1960; Széchy *et al.* 2012; Camacho *et al.* 2014). For morphological analysis, material was fixed in 4% formaldehyde. Specimens were deposited in the Herbarium FLOR at the Federal University of Santa Catarina, Brazil (FLOR60200, FLOR60201, FLOR60203, FLOR60204, FLOR60205), and in the Herbarium HUNI at the Federal University of Rio de Janeiro state (HUNI4201, HUNI4202, HUNI4498, HUNI4499). For molecular analysis, *Sargassum* specimens were cleaned by the removal of epiphytes and associated fauna and stored in silica gel. Specimen data,

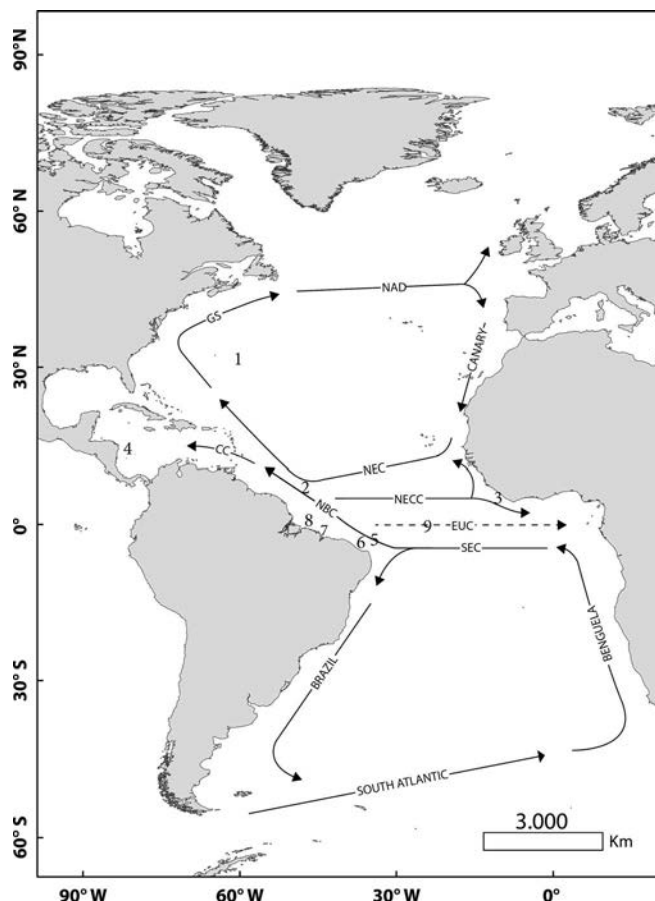


Fig. 1. Atlantic Ocean map and main oceanic currents. The numbers represent the chronological occurrence of floating *Sargassum*. 1. Sargasso Sea (Gavio & King 2011); 2. Offshore northern Brazilian coast (Széchy *et al.* 2012); 3. Sierra Leone to Ghana (Johnson *et al.* 2013); 4. San Andrés (Gavio *et al.* 2014); 5. Fernando de Noronha Archipelago (present study); 6. Rocas Atoll (present study); 7. Maranhão (present study); 8. Pará (present study); 9. São Pedro e São Paulo Archipelago (present study). CC, Caribbean Current; EUC, Equatorial Undercurrent; GS, Gulf Stream; NAD, North Atlantic Drift; NBC, North Brazil Current; NEC, North Equatorial Current; NECC, North Equatorial Countercurrent; SEC, South Equatorial Current.

including voucher number, sampling locations and GenBank accession numbers, are located in supplementary data Table S1. Epiphytic macroalgae and associated fauna were identified in the field.

DNA was extracted with the NucleoSpin Plant II kit (Macherey-Nagel, Düren, Germany) according to the manufacturer’s protocol. Molecular markers were PCR-amplified in a final volume of 50 µl: 1× PCR buffer, 1.5 mM MgCl₂, 0.2 mM of each dNTP, 0.2 mM of each primer, 5–10 ng of total DNA and 1.25 U *Taq* DNA polymerase (Invitrogen, Carlsbad, California USA). Amplifications of ITS2 were performed using the primers 5.8S-BF (5’CGATGAAGAACGCAGCGAAATGCGAT 3’) and 25BR-2 (5’TCCTCCGCTTAGTATATGCTTAA 3’), described in Yoshida *et al.* (2000). The cycle used was 94°C for 2 min, 35 cycles at 94°C for 20 s, 55°C for 30 s, 72°C for 30 s, and a final extension at 72°C for 10 min in a gradient thermal cycler (Techne TC-512, TechgeneTechne, Burling-

ton, Ontario, Canada). Amplified products were purified with the GFX PCR and Gel Band Purification DNA kit (GE Healthcare, Buckinghamshire, UK) according to the manufacturer's protocol. Sequencing reactions were performed with BigDye Terminator v3.1 Sequencing Kit (Applied Biosystems, Carlsbad, California USA) according to the manufacturer's protocol using the same PCR primers. Samples were sequenced on the automatic DNA sequencer ABI 3730 Genetic Analyzer (Applied Biosystems).

ITS2 sequences were assembled in BioEdit v7.1 (Hall 1999). Consensus sequences were aligned under MUSCLE v3.8.31 (Edgar 2004) on SeaView v4.2 (Gouy *et al.* 2010). Fifty-nine consensus sequences were assembled in a matrix of 618 base pairs, excluding PCR primers, from which 11 samples were from Brazil (Table S1). Neighbour-joining analysis was run in Seaview v4.2 with 1000 bootstrap replicates. Model evolution for the alignment was performed in jModelTest v2 (Darriba *et al.* 2012), and the selected model was GTR+G, $G = 0.5809$ [nucleotide frequency (0.1614 0.2455 0.3538 0.2394), rate matrix (3.3349 5.9266 1.7475 0.6499 5.9118 1.0000)]. Maximum likelihood analysis was performed in PhyML v3.0 (Guindon *et al.* 2010) with 100 bootstrap replicates. FigTree v1.3.1 (Rambaut 2009) was used to assemble the phylogenetic tree. *Sargassum thunbergii* (Mertens *ex* Roth) Kuntze from Japan was used as the out-group. Genetic pairwise distance was calculated in MEGA v6.0 (Tamura *et al.* 2011) (Table S2).

The stranded *Sargassum* at Atalaia beach, northeastern Amazonian coast (0°35'32"S, 47°18'30"W) was estimated during four events of massive accumulation: 3 and 24 May 2014 and 16 April and 9 May 2015. Trucks from the Salinópolis municipality removed the algae during the 2014 events. The volume of each truckload was multiplied by the number of removals to obtain the whole algal volume. During 2015, we used the following transect method: during the low tide, a 1-m² square was placed inside seven perpendicular transects (from the upper littoral to the water) with a distance of 30 m from each other. The distance between each transect was 600 m, and the number of analyzed squares in each transect depended on the beach width (4–10 squares). All the algae inside the squares were rinsed in seawater to remove the sand before weighing.

Blades and lateral branches ($n = 60$) were individually measured and weighed after air-drying for 5 min to calculate a volume–wet weight regression equation. A wet–dry weight regression was also calculated after drying the blades and branches at 65°C for 48 h. The total volume (V) obtained from the truckloads during the 2014 strandings as converted to wet weight (Ww) through the following equation:

$$Ww = 1.1605V + 1.2183 \quad (r^2 = 0.9647).$$

The wet weight was converted to dry weight (Dw) by the following equation:

$$Dw = 0.132Ww + 0.1301 \quad (r^2 = 0.9645).$$

In order to assess the origin of *Sargassum* that arrived off the Brazilian coast, images were obtained from 1 to 10 March and from 1 to 10 April 2015 by the Moderate Resolution Imaging Spectroradiometer (MODIS). MODIS Aqua 250m level 1 radiance images (band 1, 645 nm; band 2, 859 nm)

were downloaded from NASA Landsweb. The specified area was 10°N–10°S and 50°W–30°W with considerable overlap beyond this.

The oceanographic characteristics were evaluated using a NOAA data bank [surface current: data from January to April 2015, <http://www.oscar.noaa.gov>; sea surface temperatures (SST): data from 1 March to 1 May 2015; <http://www.coralreefwatch.noaa.gov/satellite/bleaching5km/index>].

RESULTS

Sargassum natans and *S. fluitans* were morphologically identified among the algae collected from Pará, Fernando de Noronha and São Pedro and São Paulo Archipelago. Based on ITS2 sequences, samples from Brazil grouped in a strongly supported clade with almost all the Atlantic *Sargassum* species (Fig. 2). Two Brazilian samples (*Sargassum* sp. MTS14 and *Sargassum* sp. MTS29) from benthic populations, from Rio de Janeiro state, were also genetically similar to the drift material that arrived in Brazil. Genetic distances within clade A, which grouped different species from the western Atlantic Ocean, were very low (0%–3%; Table S2). The ITS2, commonly used as a marker for *Sargassum* species (Camacho *et al.* 2014; Mattio *et al.* 2008), was not variable enough to distinguish among closely related *Sargassum* species or different Brazilian populations. So, the identification of *Sargassum* to species level based on morphological features is questionable. Because of the discrepancy between morphological data and molecular biological data, the material included in Table 1 is given as *Sargassum* sp. Deeper analyses have to be done that consider more samples from other localities and other genetic markers.

Epiphytes that were identified included *Oscillatoria* sp. (Cyanobacteria), *Sphacelaria tribuloides* Meneghini (Phaeophyceae), *Cladophora* sp. (Chlorophyta), *Ceramium* spp. and *Pneophyllum fragile* Kützinger (Rhodophyta). The invertebrates, *Portunus* sp. (Decapoda) and *Lepas* sp. (Pedunculata), and the fish, *Canthidermis maculate* (Bloch 1786), were identified in material from Fernando de Noronha Archipelago. The latter species is a new record for the locality (Floeter *et al.* 2008).

Total biomass from the Atalaia beach in dry weight was 23.1 and 30.8 tons for the 2014 events and 179.62 and 121.64 tons for 2015, confirming the intensity of the algal bloom during 2015 along the northern Brazilian coast. Because of its location in the far north, around 1400 and 1843 tons of *Sargassum* spp. wet weight were stranded on 16 April and 9 May 2015, respectively, on the Atalaia beach.

Satellite images from 1 to 10 March show no evidence of *Sargassum* moving outside the prospected area (Figs 3–12). Images from 1 to 10 April show higher concentrations, with many slicks in an area centralised at 10.6°N and 50.7°W (Figs 13, 14).

The SST from 26 March to 1 May 2015, a period in which the floating *Sargassum* were observed on the Brazilian coast, showed temperatures higher than the average from January to May of the same year (Fig. S1). Surface current data for a

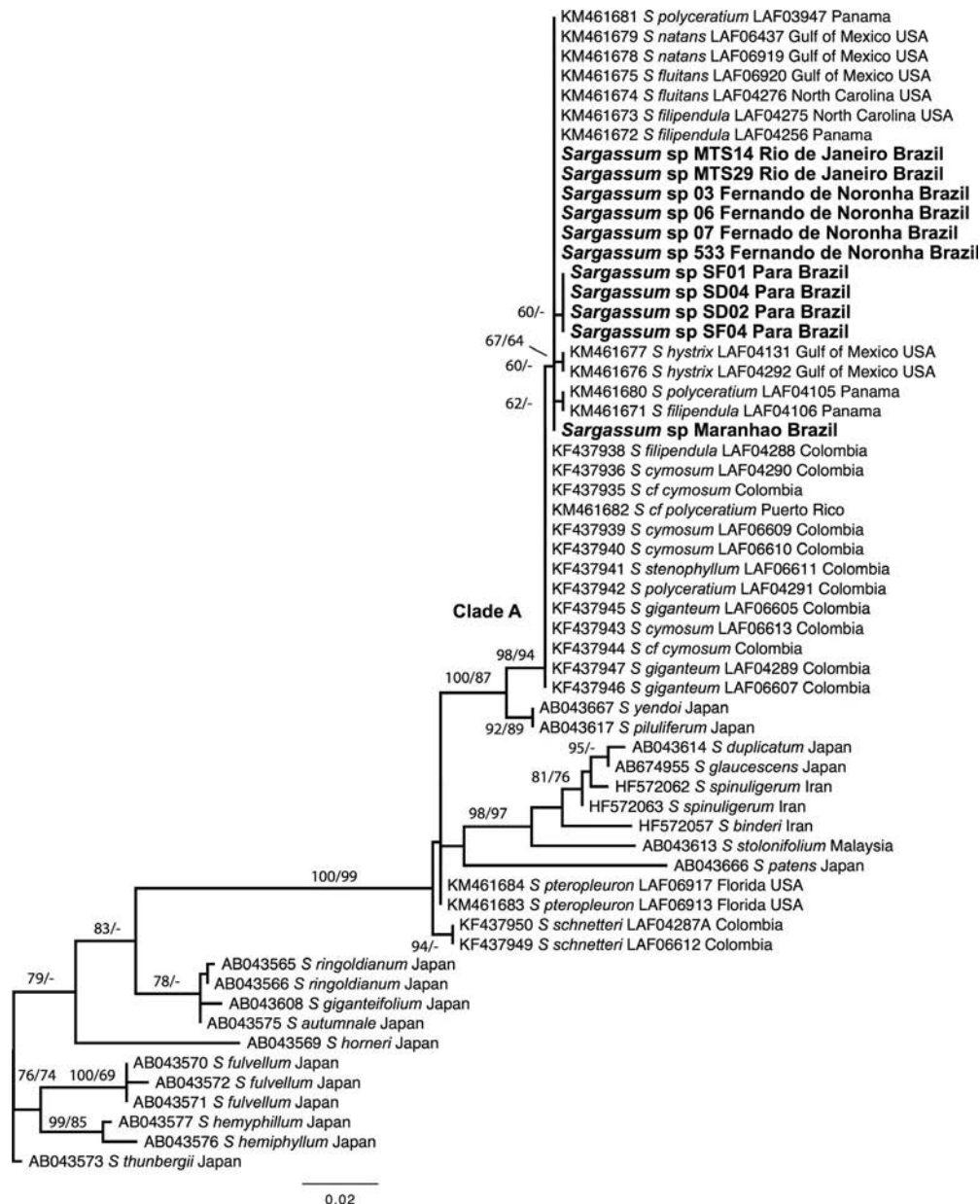


Fig. 2. Maximum likelihood phylogram based on ITS2 data set. Numbers on branch nodes are maximum likelihood/neighbour-joining bootstrap values. Scale bar represents the number of substitutions. Names in bold are sequences from material collected in Brazilian waters. Sequences of the Panama and Colombia materials are from the Atlantic side.

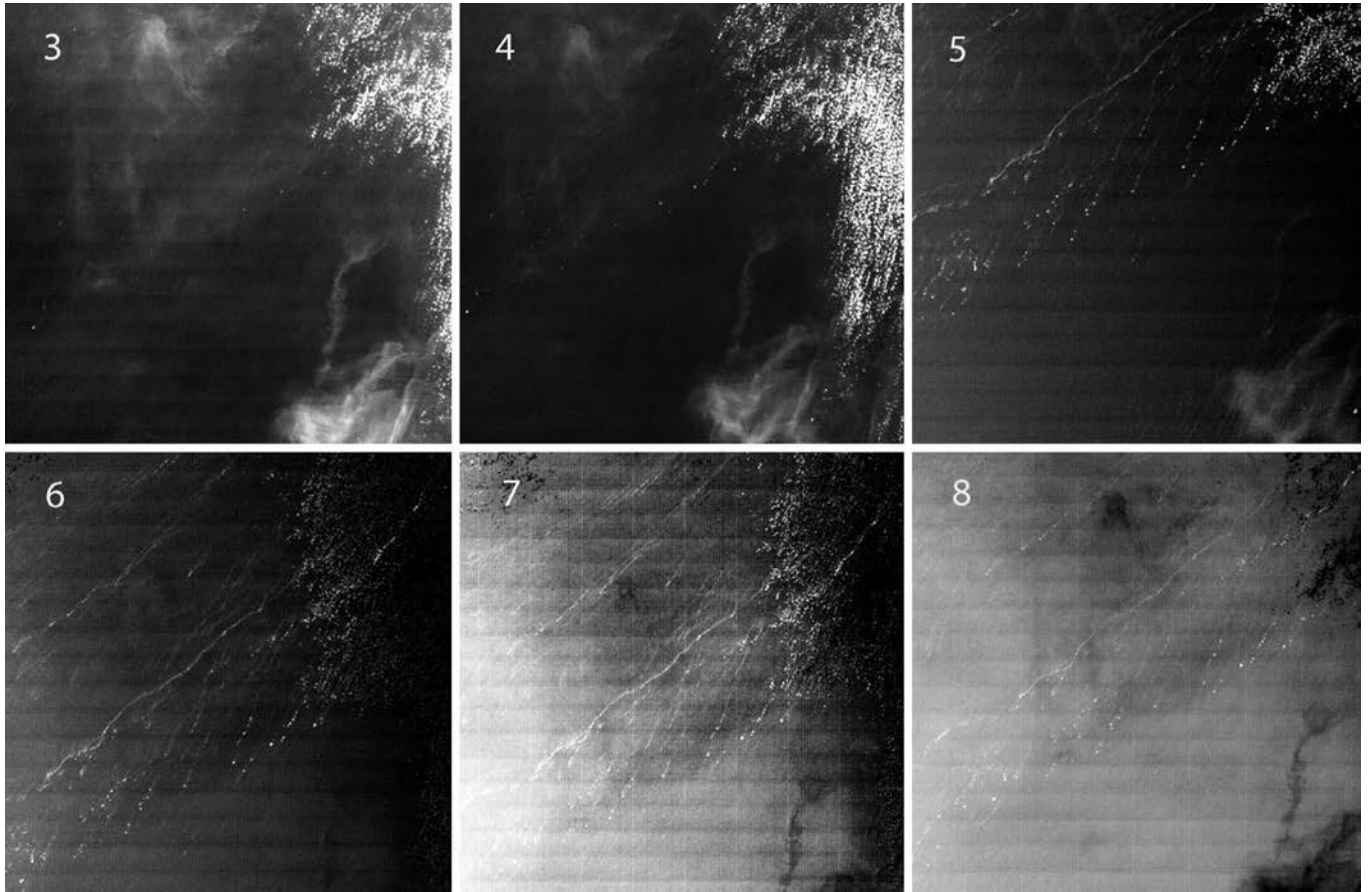
5-d interval, centred on 2 April 2015, revealed a weak (~0.2 m s⁻¹) South Equatorial Current (Fig. S2).

DISCUSSION

The absence of slicks moving from north to south strengthens the hypothesis of a matrix of pelagic *Sargassum* in the South Atlantic (Figs 3–14). Gower & King (2011), based on seven consecutive years of satellite mapping of pelagic *Sargassum*, revealed that the algae in the Gulf of Mexico do not come from the Sargasso Sea, as previously thought. These authors suggested that the southern matrix of *Sargassum* originates in the Gulf of Mexico, spreading over the Atlantic Ocean.

Latter, Smetacek & Zingone (2013) proposed that these rafters had developed off the northern Brazilian coast, north of the Amazon River mouth, from where they moved east to west through the Southern Equatorial Current, eventually stretching from shore to shore.

An alternative hypothesis to explain the accumulation of this biomass should also be considered as a combination of physicochemical seawater conditions and biological interactions. Warmer SST (Fig. S1) combined with nutrient-enriched oceans, due to continental runoff, with urban and agroindustrial sources, can provide maximum growth rates leading to eventual blooms (Cronin & Hay 1996; McCook 1999). The low pressure of herbivory in open waters may favour the maintenance of floating biomasses. Additionally,



Figs 3–8. Satellite images from 10°N–10°S and 50°W–30°W suggest no evidence of *Sargassum* moving outside the North Atlantic Ocean. **Figs 3, 4.** Images of an area about 180 km across centred at 5.2°N and 32.4°W on 2 April 2015 showing open water with cloud and haze. *Sargassum* patches are faintly visible in Fig. 1 (band 1, 645 nm) and more visible in Fig. 2 (band 2, 859 nm). **Figs 5–8.** Band difference images of an area about 180 km across centred at 5.2°N and 32.4°W on 2 April 2015 showing patterns of *Sargassum* slicks, cloud and haze. **Fig. 5.** With bands of equal weight. **Fig. 6.** Band 1 multiplied by 1.1. **Fig. 7.** Band 1 multiplied by 1.2. **Fig. 8.** Band 1 multiplied by 1.4.

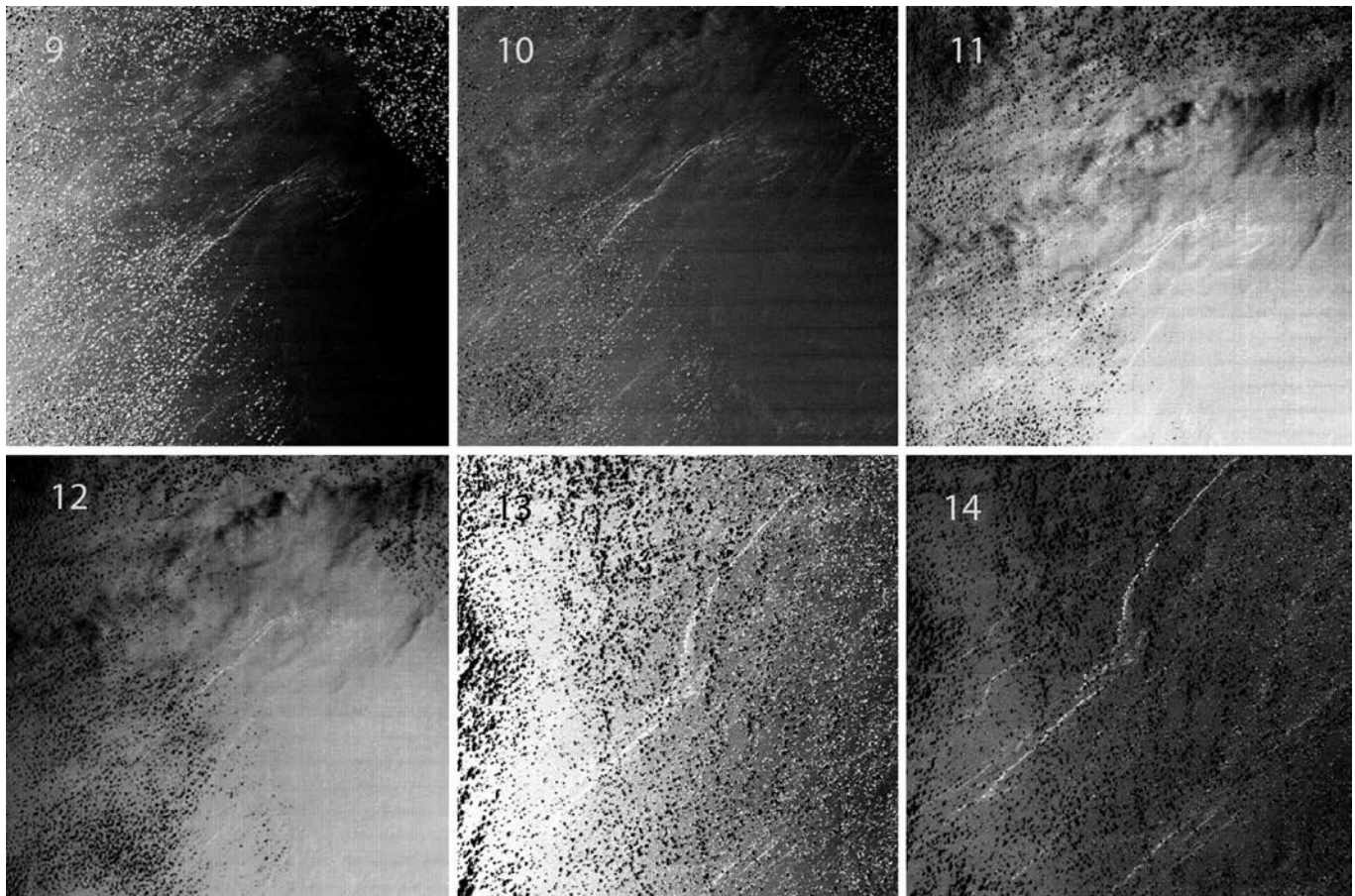
it should be stated that alterations in surface circulation patterns in the Atlantic (Beal *et al.* 2011) could be responsible for the observed *Sargassum* strandings in 2015 in new areas. The relative changes in the South Equatorial Current, based on satellite observations and data from PIRATAS buoys of previous years, as well in the surface winds, could permit the accumulation of Sargasso Sea algae to drift to new areas. Eventually, the combination of all above hypotheses results in the *Sargassum* phenomenon that is changing many key environments in Africa and South and Central America (Lyons *et al.* 2014; Martins *et al.* 2016).

A second explanation is that these algal rafts were or are being produced along the West African coast. The alternative hypothesis of *Sargassum* originating from the Mexican coast should be considered with caution, as we did not observe evidence of drift from north to south in the event of 2015. The occurrence of a similar phenomenon in Ghana in the summer of 2014 (Johnson *et al.* 2013), with similar composition, can be explained by the existence of a Sargasso Sea in low latitudes (Smetacek & Zingone 2013). However, the source of this

phenomenon is still unknown, and the connection among these events requires more information; this may be provided by a molecular biology study of *Sargassum* from each locality. Future studies should attempt to use more variable molecular markers, such as microsatellites, to elucidate the origin of floating *Sargassum* in the South Atlantic.

Considering the huge biomass of these floating *Sargassum* islands, their presence in shallow areas can be an additional source of environmental stress, as they can produce similar impacts as red and green tides in eutrophic waters (Anderson 1989; Smetacek & Zingone 2013). These masses can prevent irradiance, increase oxygen demand and eventually synthesise and release chemical compounds with allelopathic properties (Bazes *et al.* 2009).

The management of *Sargassum* biomass should be considered with caution since these communities have ecological, evolutionary (Suarez-Castillo *et al.* 2013) and economic (Kirkman & Kendrick 1997) importance, and its complete suppression can cause negative impacts with unknown consequences to related communities. Evaluations



Figs 9–12. Band difference images of an area about 180 km across centred at 5.6°N and 34.7°W on 2 April 2015 showing patterns of *Sargassum* slicks, cloud and haze.

Fig. 9. With bands of equal weight.

Fig. 10. Band 1 multiplied by 1.1.

Fig. 11. Band 1 multiplied by 1.2.

Fig. 12. Band 1 multiplied by 1.4.

Figs 13, 14. Band difference images of an area about 180 km across centred at 7.3°N and 36.0°W on 2 April 2015 showing patterns of *Sargassum* slicks, cloud and haze.

Fig. 13. With bands of equal weight.

Fig. 14. Band 1 multiplied by 1.1.

accomplished in the Caribbean showed that there is not a single approach to correct management, and local discussions should be accomplished that reflect socioenvironmental perspectives. Therefore, an environmental monitoring plan has to be drawn that considers the functioning resilience of local systems and preserves the ecological and evolutionary role of the Sargasso Sea dynamic. O₂ concentration and the abundance of biomass washed ashore should be managed until dissolved O₂ in shallow areas has been normalised. Agencies in the Caribbean (both governmental and nongovernmental), where the phenomenon is older and occurs more frequently, emphasise the importance of managing each site affected by *Sargassum*. They recognize the need for appropriate management based on its natural characteristics, and includes impact on tourism and fishing (Hinds *et al.* 2016). Governments located in the South Atlantic (South America and Africa) should invest in a long-term monitoring program covering all Atlantic-affected nations. Joint multi-

national efforts can transform the current environmental crisis into opportunities for the scientific community as well as for different sectors of the global economy. This highlights the importance of preserving the goods and services that floating *Sargassum* likely provides to the long-term resilience of biodiversity in the Atlantic Ocean.

ACKNOWLEDGEMENTS

Financial support was provided by CNPQ (National Council for Scientific and Technological Development) (PROSPEC-MAR 458548/2013-8). M.N.S. was granted with a scholarship from CNPq (383753/2014-7). P.H. thanks the CNPq grant as well as CNPq/PROTAX, Coordination for the Improvement of Higher Education Personnel (CAPES), Fundação de Amparo à Pesquisa e Inovação do Estado de Santa Catarina (FAPESC), PELD and Fundação Grupo



Figs 15–18. Arrival of floating *Sargassum* on the Brazilian coast.

Figs 15, 16. Fernando de Noronha Archipelago in April 2015 (photos: I. Escote and M.N. Sissini).

Figs 17, 18. Pará state (photos: J.E. Martinelli-Filho).

Boticário de Proteção à Natureza for financial support. M.C.O. thanks CNPq and Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) for financial support. The authors also thank the opportunities provided by INCT REDECLIMA, REBENTOS and CORAL VIVO for providing network maintenance and developing.

DEDICATION

We dedicate this work to the coauthor, friend and exemplary phycologist, Rafael Riosmena-Rodríguez.

SUPPLEMENTARY DATA

Supplementary data associated with this article can be found online at <http://dx.doi.org/10.2216/16-92.1.s1>.

REFERENCES

- ANDERSON D.M. 1989. Toxic algal blooms and red tides a global perspective. In: *Red tides* (Ed. by T. Okaichi, D.M. Anderson & T. Nemoto), pp. 11–16. Elsevier, New York.
- BAZES A., SILKINA A., DOUZENEL P., FAÏ F., KERVAREC N., MORIN D., BERGE J.P. & BOURGOUNGNON N. 2009. Investigation of the antifouling constituents from the brown alga *Sargassum muticum* (Yendo) Fensholt. *Journal of Applied Phycology* 21: 395–403.
- BEAL L.M., RUIJTER W.P.M., BIASTOCH A., ZAHAN R. & SCOR/WCRP/IAPSO WORKING GROUP 136. 2011. On the role of the Agulhas system in ocean circulation and climate. *Nature* 472: 429–436.
- BLOCH M.E. 1786. *Naturgeschichte der ausländischen Fische*, vol. 2. Siebenter Theil, Berlin. 428 pp.
- BUTLER J.N., MORRIS B.F., CADWALLADER J. & STONER A.W. 1983. *Studies of Sargassum and the Sargassum community*. Bermuda Biological Station Special Publication 22. Bermuda Biological Station for Research, St. George, Bermuda. 307 pp.

- CAMACHO O., MATTIO L., DRAISMA S., FREDERICQ S. & DIAZ-PULIDO G. 2014. Morphological and molecular assessment of *Sargassum* (Fucales, Phaeophyceae) from Caribbean Colombia, including the proposal of *Sargassum giganteum* sp. nov., *Sargassum schmetterli* comb. nov. and *Sargassum* section *Cladophyllum* sect. nov. *Systematics and Biodiversity* 13: 105–130.
- CRONIN G. & HAY M.E. 1996. Effects of light and nutrient availability on the growth, secondary chemistry, and resistance to herbivory of two brown seaweeds. *Oikos* 77: 96–106.
- DARRIBA D., TABOADA G.L., DOALLO R. & POSADA D. 2012. jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* 9: 772.
- EDGAR R.C. 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32: 1792–1797.
- FERREIRA C.E.L., JUNQUEIRA A.O.R., VILLAÇA M.C. & LOPES R.M. 2009. Marine bioinvasions in the Brazilian Coast: brief report on history of events, vectors, ecology, impacts and management of non-indigenous species. In: *Biological invasions in marine ecosystems* (Ed. by G. Rilov & J.A. Crooks), pp. 459–477. Springer, Berlin.
- FLOETER S.R., ROCHA L.A., ROBERTSON D.R., JOYEUX J.C., SMITH-VANIZ W.F., WIRTZ P., EDWARDS A.J., BARREIROS J.P., FERREIRA C.E.L., GASPARINI J.L., BRITO A., FALCÓN J.M., BOWEN B.W. & BERNARDI G. 2008. Atlantic reef fish biogeography and evolution. *Journal of Biogeography* 35: 22–47.
- GAVIO B., RINCÓN-DÍAZ M.N. & SANTOS-MARTÍNEZ A. 2015. Massive quantities of pelagic *Sargassum* on the shores of San Andres Island, Southwestern Caribbean. *Acta Biologica Colombiana* 20: 239–241.
- GOUY M., GUINDON S. & GASCUEL O. 2010. SeaView version 4: a multiplatform graphical user interface for sequence alignment and phylogenetic tree building. *Molecular Biology and Evolution* 27: 221–224.
- GOWER J.F.R. & KING S.A. 2011. Distribution of floating *Sargassum* in the Gulf of Mexico and the Atlantic Ocean mapped using MERIS. *International Journal of Remote Sensing* 32: 1917–1929.
- GOWER J.F.R., YOUNG E. & KING S.A. 2013. Satellite images suggest a new *Sargassum* source region in 2011. *Remote Sensing Letters* 4: 764–773.
- GUINDON S., DUFAYARD J.F., LEFORT V., ANISIMOVA M., HORDIJK W. & GASCUEL O. 2010. New algorithms and methods to estimate maximum-likelihood phylogenies: assessing the performance of PhyML 3.0. *Systematic Biology* 59: 307–321.
- GUIRY M.D. & GUIRY G.M. 2016. *AlgaeBase*. World-wide electronic publication, National University of Ireland, Galway. <http://www.algaebase.org>; searched on 13 January 2016.
- HALL T.A. 1999. BioEdit: a user-friendly biological alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41: 95–98.
- HINDS C., OXENFORD H., CUMBERBATCH J., FARDIN F., DOYLE E. & CASHMAN A. 2016. Golden Tides: Management best practices for influxes of *Sargassum* in the Caribbean with a focus in clean-up. CERMES, SPAW-RAC, GCFI. 17 pp.
- JOHNSON D.R., KO D.S., FRANK J.S., MORENO P. & SANCHEZ-RUBIO G. 2013. The *Sargassum* invasion of the Eastern Caribbean and dynamics of the Equatorial North Atlantic. Proceedings of the 65th Gulf and Caribbean Fisheries Institute, 5–9 November 2012, Santa Marta, Colombia, pp. 102–103.
- KIRKMAN H. & KENDRICK G.A. 1997. Ecological significance and commercial harvesting of drifting and beach-cast macroalgae and seagrasses in Australia: a review. *Journal of Applied Phycology* 9: 311–326.
- LAFFOLEY D.D'A., ROE H.S.J., ANGEL M.V., ARDRON J., BATES N.R., BOYD I.L., BROOKE S., BUCK K.N., CARLSON C.A., CAUSEY B., CONTE M.H., CHRISTIANSEN S., CLEARY J., DONNELLY J., EARLE S.A., EDWARDS R., GJERDE K.M., GIOVANNONI S.J., GULICK S., GOLLOCK M., HALLETT J., HALPIN P., HANEL R., HEMPHILL A., JOHNSON R.J., KNAP A.H., LOMAS M.W., MCKENNA S.A., MILLER M.J., MILLER P.I., MING F.W., MOFFITT R., NELSON N.B., PARSON L., PETERS A.J., PITT J., ROUJA P., ROBERTS J., ROBERTS J., SEIGEL D.A., SIUDA A.N.S., STEINBERG D.K., STEVENSON A., SUMAILA V.R., SWARTZ W., THORROLD S., TROTT T.M., & VATS V. 2011. *The protection and management of the Sargasso Sea: the golden floating rainforest of the Atlantic Ocean. Summary science and supporting evidence case*. Sargasso Sea Alliance. 44 pp.
- LUIZ O.J., ALLEN A.P., ROBERTSON D.R., FLOETER S.R. & MADIN J.S. 2015. Seafarers or castaways: ecological traits associated with rafting dispersal in tropical reef fishes. *Journal of Biogeography* 42: 2323–2333.
- LYONS D.A., ARVANITIDIS C., BLIGHT A.J., CHATZINIKOLAOU E., GUY-HAIM T., KOTTA J., ORAV-KOTTA H., QUEIROS A.M., RILOV G., SOMERFIELD P.J. & CROWE T.P. 2014. Macroalgal blooms alter community structure and primary productivity in marine ecosystems. *Global Change Biology* 20: 2712–2724.
- MARTINS M.S., MASSOCATO T.F., HORTA P.A. & BARUFI J.B. 2016. First record of red macroalgae bloom in Southern Atlantic Brazil. *Algae* 31: 33–39.
- MATTIO L., PAYRI C.E., STIGER-POUVREAU V. 2008. Taxonomic revision of *Sargassum* (Fucales, Phaeophyceae) from French Polynesia based on morphological and molecular analyses. *Journal of Phycology* 44: 1541–1555.
- MCCOOK L.J. 1999. Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef. *Coral Reefs* 18: 357–367.
- MOREIRA A. & ALFONSO, G. 2013. Inusual arribazón de *Sargassum fluitans* (Børgesen) Børgesen en la costa centro-sur de Cuba. *Revista de Investigación Marina* 33: 17–20.
- RAMBAUT A. 2009. FigTree: tree figure drawing tool, version 1.2.2. <http://tree.bio.ed.ac.uk/software/figtree>.
- SEHEIN T., SIUDA A.N., SHANK T.M. & GOVINDARAJAN A.F. 2014. Connectivity in the slender *Sargassum* shrimp (*Latreutes fuco-rum*): implications for a Sargasso Sea protected area. *Journal of Plankton Research* 36: 1408–1412.
- SMETACEK V. & ZINGONE A. 2013. Green and golden seaweed tides on the rise. *Nature* 504: 84–88.
- SOLARIN B.B., BOLAJI D.A., FAKAYODE O.S., AKINNINGBAGBE R.O. 2014. Impacts of an invasive seaweed *Sargassum hystrix* var. *fluitans* (Børgesen 1914) on the fisheries and other economic implications for the Nigerian coastal waters. *Journal of Agriculture and Veterinary Science* 7: 2319–2380.
- SUAREZ-CASTILLO A. N., RIOSMENA-RODRÍGUEZ R., ROJO AMAYA M., TORRE COSIO J., RIOJA NIETO R., WEAVER A.H., PFISTER T., HERNÁNDEZ CARMONA G., HINOJOSA ARANGO G., ABURTO OROPEZA O. & FIGUEROA CÁRDENAS A.L. 2013. Bosques de algas pardas en el golfo de California: *Sargassum*, un hábitat esencial. *CONABIO. Biodiversitas* 108: 12–16.
- SZÉCHY M.T.M., GUEDES P.M., BAETA-NEVES M.H. & OLIVEIRA E.N. 2012. Verification of *Sargassum natans* (Linnaeus) Gaillon (Heterokontophyta: Phaeophyceae) from the Sargasso Sea off the coast of Brazil, western Atlantic Ocean. *Check List* 8: 638–641.
- TAMURA K., PETERSON D., PETERSON N., STECHER G., NEI M. & KUMAR S. 2011. MEGA5: Molecular evolutionary analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Molecular Biology and Evolution* 28: 2731–2739.
- TAYLOR W.R. 1960. *Marine algae of the eastern tropical and subtropical coasts of the Americas*. University of Michigan Press, Ann Arbor. 870 pp.
- THIEL M.A. & GUTOW L. 2005. The ecology of rafting in the marine environment I. The floating substrata. *Annual Review of Oceanography and Marine Biology* 42: 181–264.
- WARNER R.M. 2014. Conserving marine biodiversity in the global marine commons: co-evolution and Interaction with the law of the sea. *Frontiers in Marine Science* 1: 1–23.
- YOSHIDA T., STIGER V. & HORIGUCHI T. 2000. *Sargassum boreale* sp. nov. (Fucales, Phaeophyceae) from Hokkaido, Japan. *Phycological Research* 48: 125–131.

Received 20 July 2016; accepted 24 November 2016
Associate Editor: Charles Yarish