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New records of seaweeds and filamentous cyanobacteria from Trindade Island: an updated checklist to support conservation guidelines and monitoring of environmental changes in the southern Atlantic archipelagos

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Summary: Oceanic islands are natural laboratories for investigating species diversity and richness patterns. Changes in abiotic parameters may induce shifts in marine biota. Seaweeds are recognized as bioindicators, though those from remote tropical islands have been rarely studied. This study updates the diversity, richness and distribution of macroalgae from Trindade, a Brazilian volcanic island located 1140 km off the coast. Biotic data, obtained in a global database and in situ and compiled in a new records list, were associated with abiotic parameters. Conservation and ecological issues were discussed in the context of the observed greater richness, expansion of the distributional range and low endemism. A total of 141 species were identified, including 60 new records and 20 taxa of filamentous cyanobacteria. The greater richness, including potential cryptogenic species, may primarily be associated with past incomplete samplings, current new techniques and combined taxonomical methods, including molecular analysis for cryptic species. However, on the macroscale, this study provides information for the re-evaluation of aspects of endemism, connections and biogeographical distribution shifts of seaweed assemblages, considering environmental changes. In addition, this updated checklist establishes a baseline for further comparative studies, reinforcing the hypothesis that biogeographical isolation can be disrupted by meteorological and oceanographic shifts, altering dispersal patterns and resulting in higher ecosystems connectivity.

Keywords: benthic algae; diversity monitoring; remote islands; taxonomy; marine conservation; climate change.

Nuevos registros de algas marinas y cianobacterias filamentosas de la isla Trindade: una lista de verificación actualizada para apoyar las pautas de conservación y el monitoreo de los cambios ambientales en los archipiélagos del Atlántico sur

Resumen: Las islas oceánicas son laboratorios naturales para investigar la diversidad de especies y los patrones de riqueza. Los cambios en los parámetros abióticos pueden inducir cambios en la biota marina. Las algas son reconocidas como bioindicadores, aunque rara vez se han estudiado las de las islas tropicales remotas. Este estudio actualiza la diversidad, riqueza y distribución de macroalgas de Trindade, una isla volcánica brasileña ubicada a 1140 km de la costa. Los datos bióticos, obtenidos en una base de datos global e in situ, compilados en una nueva lista de registros, se asociaron con parámetros abióticos. Los temas ecológicos y de conservación se discutieron en el contexto de la mayor riqueza observada, la expansión del rango de distribución y el bajo endemismo. Se identificaron un total de 141 especies, incluidos 60 nuevos registros y 20 taxones de cianobacterias filamentosas. La mayor riqueza, incluidas las especies criptogénicas potenciales, puede estar asociada principalmente con muestreos incompletos del pasado, nuevas técnicas actuales y métodos taxonómicos combinados, incluido el análisis molecular de especies crípticas. Sin embargo, en la macroescala, este estudio proporciona información para la reevaluación de aspectos de endemismo, conexiones y cambios en la distribución biogeográfica de los conjuntos de algas marinas, considerando los cambios ambientales. Además, esta lista de verificación actualizada establece una línea de base para futuros estudios comparativos, lo que refuerza la hipótesis de que el aislamiento biogeográfico puede verse afectado por cambios meteorológicos y oceanográficos, alterando los patrones de dispersión y dando como resultado una mayor conectividad de los ecosistemas.

Palabras clave: algas bentónicas; monitoreo de la diversidad; islas remotas; taxonomía; conservación marina; cambio climático.

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INTRODUCTION

Oceanic islands, bathed by oligotrophic waters, are considered to be ecosystems with unexplored biodiversity and high endemism of several groups of marine organisms. Some remote and isolated islands are less influenced by anthropogenic impacts than coastal islands. These ecosystems are considered peculiar and pristine natural habitats, showing environmental transitional features that result in easily interpretable biogeographic and ecological patterns (Borregaard et al. 2016, Pellizzari et al. 2017). Moreover, oceanic islands are examples of disjunctions or hypothetical oceanographic discontinuities across a biogeographic transitional zone. Distinct hydrographic features promote physical breaks that can influence dispersal and connectivity between populations.

The Brazilian oceanic ecosystems are comprised of the Rocas Atol, Trindade e Martim Vaz, São Pedro e São Paulo, and Fernando de Noronha archipelagos. The focus of the present study is Trindade, a volcanic island located 1140 km off the coast of Brazil. There is much scientific interest in Trindade as an ecological model for environmental predictions and as a control area to be compared with other locations.

Seaweeds are key organisms in the sustainability of the entire trophic chain as primary producers and providers of biogenic habitats for several marine organisms. In addition, macroalgae assimilate nutrients and trace elements from seawater and are responsible for pH control (homeostasis) in the water column. For these reasons, macroalgae are sensitive bioindicators to changes in the physical and chemical patterns of seawater (Kordas et al. 2011). Studies on macroalgae diversity from Trindade Island were published by Richardson (1975), Pedrini et al. (1989) and Nassar (1994). Villaça et al. (2006) reported the last seaweed taxa compilation, listing 121 species, with 53% originating from the intertidal and shallow subtidal zones and 47% from the deeper subtidal zone.

Sea surface temperature (SST) and salinity are the main factors that determine the regional and local growth of seaweed, including at biogeographical boundaries. The variation in marine abiotic parameters may be due to natural variability as well as anthropogenic activity (Lifland 2003). The interannual variability in these parameters is the result of large-scale weather patterns, whereas anthropogenically induced variability is associated with circulation anomalies (atmospherical and marine) and abrupt changes in thermohaline and precipitation patterns.

Current global changes are inducing shifts in seaweed assemblages and ecosystem functionality (Parmesan 2006, Rosenzweig et al. 2008, Pellizzari et al. 2017). Responses to climate change are particularly rapid and strong in marine ecosystems, especially in the intertidal zone where species often reside at their upper temperature-tolerance limits (Hoegh-Guldberg and Bruno 2010, Sorte et al. 2010). The present study focuses on this zone. In oceanic ecosystems, considering abiotic shifts and their responses, species that fail to acclimatize physiologically (or evolve genetically) will either expand their distributional limits into new habitats or become extinct (Jueterbock et al. 2013).

Reports of new records, including cryptogenic species, have a temporal limit in their interpretability, considering that species may expand their distributional ranges (Occhipinti-Ambrogi 2007). This would result in geographical distribution shifts and reduction in endemism levels (Pellizzari et al. 2017, 2020, Oliveira et al. 2020), which can modify the structure of marine communities. According to Sangil et al. (2012), abrupt changes in the abiotic parameters emerge as *invasion windows* for expanding the biogeographical distribution of marine species. Guo et al. (2005) and Araújo et al. (2009) showed that distributional shifts are likely to be magnified for species from geographic boundaries, where organisms are at their ecophysiological tolerance limits. This suggests that the most effective method for predicting diversity changes is by monitoring boundary or marginal populations, such as the insular seaweed assemblages found in Trindade.

Several studies have reported changes in macroalgae diversity, mainly in coastal ecosystems (Iles et al. 2012, Duarte et al. 2013, Sjøtun et al. 2015). Insular areas have also been addressed, including studies in Tristan da Cunha (Saunders et al. 2019), Ascension (Barnes et al. 2015, Tsiamis et al. 2014), the Canary Islands (Afonso-Carrillo et al. 2007, Sanson et al. 2002, Haroun et al. 2002) and the Azores islands, located in the southern and northern zones of the Mid-Atlantic Ridge (MAR), respectively, and Trindade between Brazil and MAR. Large-scale and mainly climate-driven distributional and biogeographical changes to temperate and polar ecosystems have been broadly reported (Sjøtun et al. 2015, Pellizzari et al. 2017, 2020, Oliveira et al. 2020). In addition to these changes, new molecular techniques are being used to investigate cryptic species and reorganize the macroalgal taxonomy, establishing increasingly accurate phylogenetic relationships. Classical taxonomy, supported by molecular techniques, uses conservationist tools to monitor population shifts and highlights new ecological trends, introductions and extinctions. For example, it has been widely used as a technique for predicting and

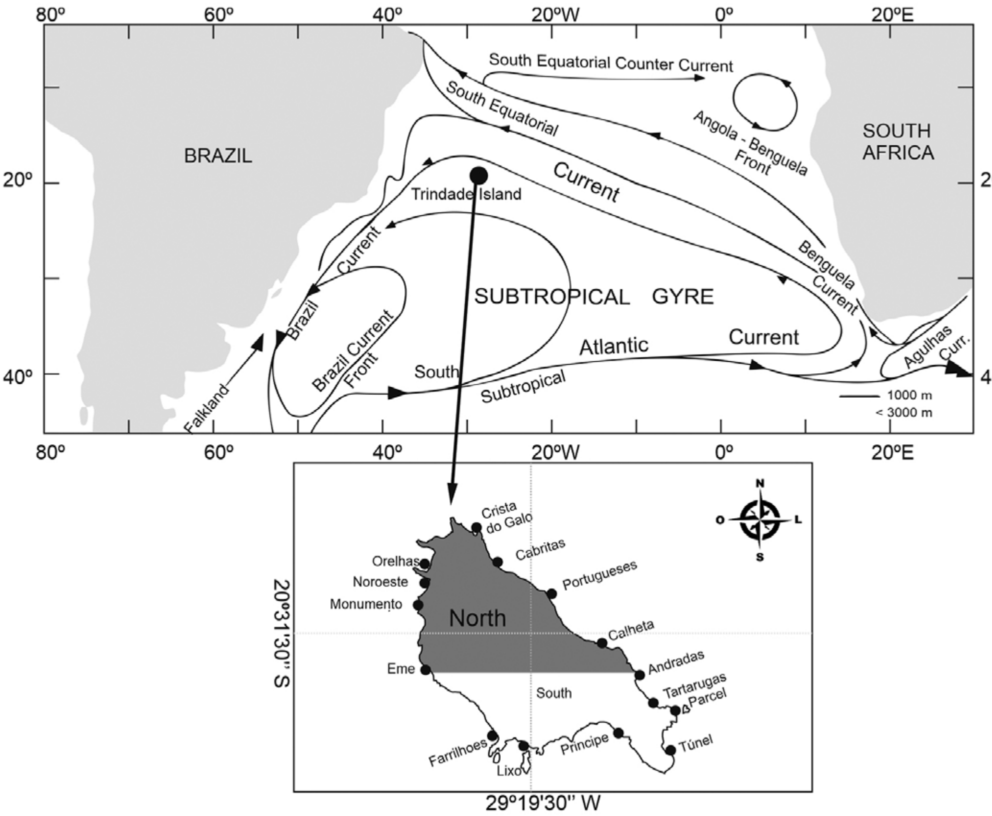

Fig. 1. – Geographic position and oceanic circulation surrounding Trindade, southwestern Atlantic Ocean (adapted from Peterson and Stramma 1991). Detailed map from the island beaches.

mitigating natural or anthropic impacts on environments. However, recent checklists and ecological assays for tropical remote islands are scarce.

This study establishes an updated seasonal checklist, presenting new records of 60 species, and demonstrates the relationship between these records and abiotic parameters to discuss new trends in marine ecology facing environmental changes. The scarcity of recent studies on seaweed diversity and the absence of a temporal approach for Trindade or any other Brazilian oceanic island justify this contribution. We also provide a baseline for further comparative studies with other Atlantic oceanic islands that aim to re-evaluate aspects of macroalgae endemism, isolation, connections and biogeographical distributional shifts. Moreover, this database will be fundamental to the establishment of environmental monitoring plans in response to climatic and oceanographic changes.

MATERIALS AND METHODS

Study area

Trindade is located at 20°30′30″S, 29°19′30″W (Fig. 1), 1140 km east of Espírito Santo State. The Archipelago of Trindade and Martim Vaz recently became a Federal Environmental Protected Area (Decree 9312/2018). In 1957, the Brazilian Navy established the Oceanographic Station of Trindade Island, which has provided support for the claim of the area as an Exclusive Economic Zone. Since 2007, the Scientific Station of Trindade Island has supported research and conservation activities on the island, as well as this project.

The island is the easternmost part of the Vitória-Trindade Ridge, an underwater volcanic chain (Almeida 2006), erected from the Atlantic abyss by mixed volcanic activity approximately three million years ago (Alves 1998). Almeida (2000, 2002) reports that Trindade, almost completely composed of volcanic and subvolcanic rocks, was formed between the end of the Pliocene and the Holocene (2.3 and 2.9 Ma). Pires et al. (2016) presented a new age proposal for the formation of Trindade, coupled with previous petrological information, allowing the volcanic history of the island to be reconstructed (i.e. 3.9-0.25 Ma), distinguishing volcanic episodes and solving previous stratigraphic uncertainties. Volcanic activity in Trindade ceased completely by 0.25 Ma.

Trindade is 5.9 km long and 2.7 km wide, and is aligned NW-SE. The emerged area encompasses 13.5 km^2 with a surrounding depth of approximately 5000 m. Five volcanic episodes gave rise to the oldest region (the north face) and a more recent region (the south face) (Calliari et al. 2016). Apart from some pyroclastic rocks, the rocks are mainly sodium-alkaline and silica rich, originating from undersaturated lavas. The coast along the island is composed of algal reefs, narrow volcanic rocky beaches, localized dunes, cones and slopes. The protrusions of volcanic rocks have formed several embayments surrounded by biogenic substrate mainly from corallinaceous algae beds. The beach lines (Fig. 2) consist of 76% rock or beachrock covered by biogenic substrate and 24% sand (Calliari et al. 2016).

Figure 3 shows the temporal thermohaline pattern during the past 14 years (August 2004-August 2018) in the surroundings of Trindade, with higher minimum temperatures (winter) and lower salinities (during winter and summer) since 2012. In 2017, anomalies for this decade were observed for both parameters.

Trindade's climate ranges from tropical semi-humid to semi-arid. The rainfall regime is random with light rain but constant during the summer; during the late autumn/winter, cold fronts periodically reach the island (Almeida 2006). The tropical climate is mitigated by the dominance of east (45%) trade winds. The annual average temperature is 25°C (maximum 32.3°C in February and minimum in August of 17.3°C). Based on the WAVEWATCH III model simulations (NOAA), waves arrive mainly from the south (33.7%) and southwest (23.4%), with an average height of 2.14 m. The tidal regime is semi-diurnal, with a micro-tidal range of 1.3 m. Calliari et al. (2016) discuss a higher frequency of meteorological fronts than previously reported, besides changes in the circulation patterns, and changes in the rainfall regime for Trindade surroundings.

Sampling methods and analysis of biological data

In contrast to other macroalgae assemblage studies along the Brazilian coast, previous studies in Trindade Island focused on the deep subtidal area, using dredged material obtained from short-term expeditions of the island surroundings. These studies mainly conducted sporadic and random samplings rather than using standardized methods.

Sampling surveys were supported by Brazilian Navy ships and occurred over four years, during the austral summer (January) and winter (July and August) of 2014, 2015, 2016 and 2017, eight cruises in total. Macroalgae and cyanobacteria specimens were sampled along 13 beaches (Fig. 1). The specimens (n=3, i.e. 3 specimens per species/beach) were collected by scraping the algal turfs and bedrock during spring tide along the intertidal zone. The cyanobacteria specimens were sorted among the collected turfs. Each site was sampled once per cruise each summer or winter. The sampling method performed at each site used quadrats (n=5, 0.5 m^2) distributed every ±20 m along a 100 m transect. The shallow subtidal area was sampled using free diving. Fertile and entire specimens were collected along quadrats of 50×50 cm (n=5) distributed in linear transects (150 m) parallel to the coastline. A remotely operated vehicle (Guardian 2.1, France) was used to locate the calcareous algae beds up to 15 m deep, fa-

Fig. 2. – Trindade island. A, Parcel and Tartarugas Beach; B, Cachoeira tide pools; C and D, Andradas and Tartarugas beachrock.

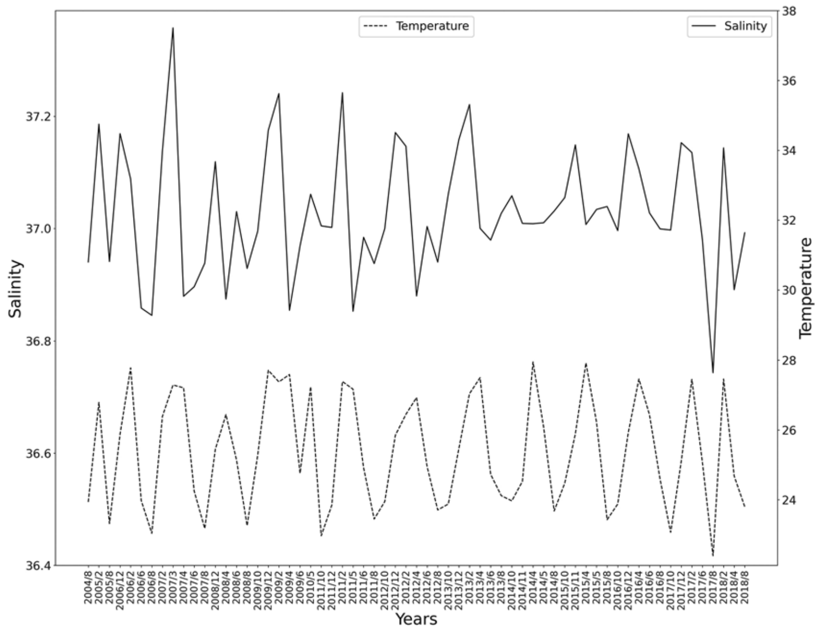

Fig. 3. – Variation in SST (°C) and salinity (psu) in the surroundings of Trindade Island from 2004 to 2018 (raw data obtained from CTD/XBT profiles performed between the Brazilian continental shelf and Trindade Island: MOVAR-GOOS (http://www.goosbrasil.org/movar).

cilitating the samplings and observations of the spatio-temporal distribution.

In the laboratory, turf and beachrock samples were sorted, washed and fixed with formalin (4% diluted in seawater), for further taxonomic analysis of the vegetative and reproductive thalli through stereoscopic and optical microscopy with phase contrast and an image capture system (Olympus CX31). External morphological features such as colour, height, shape and size of holdfast and the type of branching were observed, annotated and photographed before fixation. For internal morphological observations, the material was dissociated (filamentous) or hand-sectioned (leafy and fleshy thalli) using scalpel blades and mounted on glass slides for microscopic observation. Calcareous specimens were decalcified with 5% hydrochloric acid and sectioned to observe the reproductive structures. Cryptic species or groups, when it was possible to obtain sufficient monospecific material among the turf (Fig. 4), were conditioned in silica gel for molecular analysis, using different markers for each algal

Fig. 4. – Trindade Island turfs. These associated macroalgae form broad tangled mats, often growing on other calcareous algae (branched or crustose), along the intertidal and shallow subtidal zones. Scale=1 cm.

Table 1. – New seaweed records: temporal checklist from Trindade Island. Information of location and habitat occurrence and previous records off Trindade are provided. 1, present; 0, absent; a.b.o.i, another Brazilian oceanic island.

			Trindade		Previous Ocurrences off Trindade		
	Summer	Winter	Beach	Habitat	a.b.o.i.	Brazil Coast	Nearest occurrence off Brazil
CYANOBACTERIA							
Coleofasciculus chthonoplastes (Thuret ex Gomont) Siegesmund et al.	1	0	E	turf midlittoral	0	1	Canary Islands
Chamaecalyx sp.	1	0	T	turf midlittoral	0	1	Canary, S Portugal, Argentina
Leibleinia sp.	1	0	A	turf midlittoral	0	1	
*Sirocoleum kurzi*i Gomont	1	0	PR	turf midlittoral	0	1	Canary /Argentina
*Symploc*a sp.	1	1	A/PO	turf midlittoral	0	1	
Anabaena sp.	1	0	E	turf midlittoral	0	1	
Hydrocoryne spongiosa Schwabe ex Bornet & Flahault	1	1	A/PN	turf midlittoral	0	1	Caribbean Isls., Canary, Madeira
Nostoc commune Vaucher ex Bornet & Flahault	1	1	A/C /E/F/O	turf midlittoral	0	1	Canary /Argentina
Blennothrix lyngbyacea (Kutzing ex Gomont) Anagnostidis & Komarek	1	1	A/C	turf midlittoral	0	1	Caribbean, Canary, Madeira
Lyngbya confervoides C.Agardh ex Gomont	1	1	A/C/PN/PR	turf midlittoral	0	1	Caribbean, Canary, Madeira, Gough
Lyngbya majuscula Harvey ex Gomont	1	1	A	turf midlittoral	1	1	Canary
Oscillatoria sp.	0	1	A	turf midlittoral	1	1	
Phormidium cf. *holdenii* (Forti) Branco et al.	1	0	A	turf midlittoral	0	1	Caribbean, Canary, Madeira
Phormidium nigroviride (Thwaites ex Gomont) Anagnostidis & Komarek	1	1	A / E	turf midlittoral	0	1	Florida, Argentina, Canary
Calothrix sp.	0	1	A	turf midlittoral	0	1	
Rivularia atra Roth ex Bornet & Flahault	1	1	A/E	turf midlittoral	0	1	Caribbean/ Canary
Kyrtuthrix sp. (cf. maculans)	0	1	A	turf midlittoral	0	1	Canary
Scytonema sp.	1	0	E	turf midlittoral	0	1	
Spirulina major Kutzing ex Gomont	1	0	PO	turf midlittoral	0	1	Canary, Cuba, Argentina
Stigonema sp.	1	0	E	turf midlittoral	0	1	
Total 20	17	11					
CHLOROPHYTA							
Bryopsis hypnoides J.V.Lamouroux	1	1	A/L	upper subl., tidal pools	0	1	Canary, Azores, Caribbean
Caulerpa kempfii A.B.Joly & S.M.B.Pereira	1	1	E/A	beach rock	0	1	Caribbean
Chaetomorpha brachygona Harvey	0	1	C	midlittoral	0	1	Caribbean
Cladophora albida (Nees) Kutzing	1	1	A / O / PN	turf / beach rock	1	1	Canary, Azores, Caribbean
Cladophora brasiliana G.Martens	1	0	C / E / P	turf / beach rock	0	1	Caribbean
Cladophora catenata Kutzing	1	1	O/N	turf / beach rock	0	1	Gough Island , Caribbean
Cladophora coelothrix Kutzing	1	1	A / C / O	turf / beach rock	0	1	Ascension, St Helena
Cladophora corallicola Borgesen	1	1	A / C / P	upper subl., tidal pools	0	1	Caribbean
Cladophora dalmatica Kuttzing	1	1	A / C / F	turf / beach rock	0	1	Canary, Bermudas
Cladophora lehmanniana (Lindenberg) Kutzing	1	0	CA	turf / beach rock	0	1	Ascension, Cape Verde, Canary
Cladophora rupestris (Linnaeus) Kutzing	0	1	PN	turf / beach rock Midl.	0	1	Azores, Gough
Cladophora sericea (Hudson) Kutzing	1	1	A / E / PN	turf / beach rock Midl.	0	1	Canary Islands
Lychaete pellucida (Hudson) M.J.Wynne	1	0	A	upper subl., tidal pools	0	0	Azores, Gough, Canary, Cape Verde
Neostromatella monostromatica Wynne, Furnari & Nielsen	1	1	A / E / P	epiphyte of another algae	0	1	Canary
Parvocaulis parvulus (Solms-Laubach) Berger et al.	1	1	E / T	upper sublittoral rocks	1	1	Canary, Madeira, Caribbean
Prasiolales	0	1	A	upper eulittoral	0	0	N Atlantic, Mediterranean, New Zealand
Pseudorhizoclonium africanum (Kutzing) Boedeker	0	1	O	midlittoral	0	1	C Verde, Azores, Canary, Caribbean
Ulva chaetomorphoides (Borgesen) Hayden et al.	1	0	E	turf	0	1	Bermudas, Caribbean
Ulva clathrata (Roth) C.Agardh	1	1	A / PN	rock pools	0	1	Ascencion, Azores, Canary, Cape Verde
Ulva compressa Linnaeus	0	1	A	beachrocks,upper subl.	0	1	Ascencion, Canary, Cape Verde, Azores,
Ulva flexuosa Wulfen	1	1	A / E / PN	beachrocks,upper subl.	1	1	Ascencion, Canary, Caribbean, C Verde, Azores
Ulva linza Linnaeus	0	1	A	beachrocks,upper subl.	0	1	Caribbean, Azores, C Verde, Ascencion, Canary
Ulvella scutata (Reinke) R.Nielsen, C.J.O'Kelly & B.Wysor	1	1	A/E	epiphyte of another algae	1	1	Caribbean, Azores, Canary
Ulvella viridis (Reinke) R.Nielsen, C.J.O'Kelly & B.Wysor	1	1	A/C/E	epiphyte of another algae	1	1	Bermudas, Canary, Tristan da Cunha, Caribbean
Valonia aegagropila C.Agardh	1	1	A/E	upper subl., tidal pools	1	1	Canary
Valonia ventricosa J.Agardh	1	1	E	upper subl., tidal pools	0	1 (N)	Ascencion, Caribbean, Bermuda, C Verde, Canary
Total 26	20	22					

Table 1 (Cont.). – New seaweed records: temporal checklist from Trindade Island. Information of location and habitat occurrence and previous records off Trindade are provided. 1, present; 0, absent; a.b.o.i, another Brazilian oceanic island.

			Trindade		Previous Ocurrences off Trindade		
	Summer	Winter	Beach	Habitat	a.b.o.i.	Brazil Coast	Nearest occurrence off Brazil
PHAEOPHYCEAE							
Asterocladon rhodochortonoides (Borgesen) Uwai et al.	1	0	E	midlittoral and turf	1	1	Azores, Canary, St Helena
Dictyota ciliolata Sonder ex Kutzing	1	1	CA / E /O	rock pools, subl. rocks	1	1	Azores, Canary
Dictyota jamaicensis W.R.Taylor	1	1	E	rock pools, subl. rocks	1	1	Cape Verde; Caribbean Isls.
Ectocarpus fasciculatus Harvey	1	1	A / PN	midlittoral	0	1	Canary
Feldmannia indica (Sonder) Womersley & A.Bailey	1	1	A	beach Rock pools	1	1	Caribbean
Levringia brasiliensis (Montagne) A.B.Joly	0	1	E	beach rocks, rock pools	0	1	Ascension, Cape Verde
Padina antillarum (Kutzing) Piccone	1	0	PO / N	upper subl., tidal pools	0	1	Caribbean
Stypopodium zonale (J.V.Lamouroux) Papenfuss	1	0	E	rock pools, upper subl.	1	1	Caribbean, Ascencion, St Helena
*Sphacelaria brachygoni*a Montagne	1	1	E / PR / L	midlittoral	1	1	Cape Verde
Total 9	8	6					
RHODOPHYTA							
Amphiroa anceps (Lamarck) Decaisne	1	0	E	turf, mid/upper subl.	0	1	South Africa
Amphiroa beauvoisii J.V.Lamouroux	1	1	N	mid/upper sublittoral	1	1	Azores, Canary, St Helena
Centroceras gasparrinii (Meneghini) Kutzing	1	1	A / PN	rock pools, sublittoral	0	0	Ascension, Caribbean
Ceramium brevizonatum H.E.Petersen	1	1	A / E / PN	turf and sublittoral rocks	1	1	Caribbean Isl.
Ceramium deslongchampsii Chauvin ex Duby	1	1	E / F	turf and upper sublittoral	1	1	Azore, Canary, St Helena
Ceramium diaphanum (Lightfoot) Roth	1	1	A / C	turf and sublittoral rocks	1	1	Ascension, St Helena, Canary, Azores, Caribbean
Ceramium luetzelburgii O.C.Schmidt	1	0	E / L	turf and sublittoral rocks	1	1	Caribbean (Martinica)
Ceramium tenerrimum (G.Martens) Okamura	0	1	PN	turf and upper sublittoral	0	1	Cape Verde, Ascencion, Canary
Champia minuscula A.B.Joly & Ugadim	1	0	E / F / PO	sublittoral rocks	1	1	Caribbean
Chondracanthus acicularis (Roth) Fredericq	0	1	C	turf	1	1	Azores, Canary, Caribbean
Grateloupia cf. filicina (J.V.Lamouroux) C.Agardh	1	1	C / N / F / PN	upper sublittoral	0	1	Azores, Canary, St Helena, C Verde, Caribbean
Halymenia vinacea M.Howe & W.R.Taylor	0	1	O	sublittoral	1	1	Canary
Hildenbrandia rubra (Sommerfelt) Meneghini	1	1	E	mid till upper sublittoral	1	1	Ascension, Canary, Caribbean
Hydrolithon cf. farinosum (J.V.Lamouroux) Penrose & Chamberlain	0	1	L / O	sublittoral	0	1	Ascension, St Hel., Azores, Canary, C Verde, Caribbean
Jania capillacea Harvey	0	1	A	turf, mid and upper subl.	1	1	Ascension, Azores, Canary, St Hel., C Verde, Caribbean
Jania pumila J.V.Lamouroux	1	1	A	turf and upper subl.	1	1	Ascension, Azores, Canary, St Hel., C Verde, Caribbean
Lithophyllum prototypum (Foslie) Foslie	1	1	C	sublittoral	1	1	Caribbean
Melanothamnus tongatensis (Harvey ex Kutz.) Diaz-Tapia & Maggs	1	1	A/C/E/P	turf and upper subl.	0	0	Bermudas, Panama
Melyvonnea erubescens (Foslie) Athanasiadis & Ballantine	1	1	E	sublittoral	1	1	Caribbean, Canary, Cape verde
Palisada perforata (Bory) K.W.Nam	1	1	A / PN	mid-turf, upper subl.	1	1	Ascencion, Canary, Bermudas
Peyssonnelia sp.	1	1	C / E	mid, upper subl.	1	1	Canary, C Verde, Caribbean
Polysiphonia sertularioides (Grateloup) J.Agardh	1	0	A / E / P	mid-turf, upper subl.	0	0	Canary, Caribbean isls.
Pterocladiella sanctarum (Feldmann & Hamel) Santelices	1	1	L / PN	mid-turf, upper subl.	0	1	Caribbean isls.
Taenioma perpusillum (J.Agardh) J.Agardh	1	1	A	turf	0	1	Azores, Canary, C Verde, Caribbean
Vertebrata foetidissima (Cocks ex Bornet) Diaz-Tapia & Maggs	1	1	A/C	mid-turf, upper subl.	0	0	Azores, Caribbean, C Verde
Total 25	20	21					

group. Nomenclatural information and taxonomical status were applied following Guiry and Guiry (2020). Exsiccate vouchers of the new records were deposited in the Herbarium of the Botanical Museum of Curitiba.

Morphological taxonomic identification was performed, using as comparative material specialized and illustrated descriptions of the species from the Brazilian oceanic islands (Villaça et al. 2006, 2010, Amado-Filho et al. 2012, Burgos 2011, Burgos et al. 2009, Pereira-Filho et al. 2011, 2012, 2015); southeastern (Cordeiro-Marino 1978, Crispino 2007, Coto 2007) and northeastern Brazil (Moura 2000, Nunes 2005, Nunes and Guimarães 2008); Florida (Littler and Littler 2000, Wysor and Kooistra 2003, Dawes and Mathieson 2003), the Caribbean islands (Semidey and Suárez 2013, García and Díaz-Pulido 2006, Díez-García et al. 2013), Tristan da Cunha (Saunders et al. 2019), Santa Helena and Ascension Island (Tsiamis et al. 2014); Ascension Islands (Barnes et al. 2015); and the Canary Islands (Sanson et al. 2002, Haroun et al. 2002, Afonso-Carrillo et al. 2007).

Environmental data

SST, salinity and pH were selected as oceanographic set predictors to be compared with the biological data generated. Abiotic data were measured in situ along the sampled beaches during the winter and summer: SST and salinity were monitored using a multiparameter probe (Hexis, USA) and pH was measured by a portable pH meter. Rainfall and ultraviolet radiation data were obtained from the Trindade Island Meteorological Station database. The forecast of tidal amplitudes was obtained from the Hydrography and Navigation Office website, Brazilian Navy.

Statistical analysis

The Sorensen similarity index was used to construct a cluster dendrogram and compare the grouping and similarity/dissimilarity between faces and cruises (during summer and winter). A t-test was performed to test differences between the north and south faces. An orthogonal ANOVA was performed to test differences in seaweed richness between the north and south faces and between the summer and winter cruises. The seaweed richness data were tested for normality and transformed into log-normal data when the ANOVA constraint was not satisfied. For non-normal data, we assumed an alpha value of 0.01, as suggested by Underwood (1997). Tukey HSD was the chosen post-hoc test. All the analyses were performed using R statistical software (version 3.6.1) and R-Studio (1.2.5019) (R Core Team 2019).

RESULTS

A total of 141 macroalgae species were identified at the 13 beaches sampled in Trindade Island. Sixty species represent new records, comprising 26 species of Chlorophyta, 9 species of Phaeophyceae and 25 species of Rhodophyta (Table 1). Three putative new species of calcareous algae are under investigation. In addition, 20 species of cyanobacteria were reported in the first time to the island, totalling 161 species from the intertidal to the shallow subtidal zones (Fig. 5).

The new seaweed records from Trindade indicate higher richness of Phaeophyceae and Cyanobacteria in summer and of Chlorophyta and Rhodophyta in winter, although no significant difference was observed between the summer and winter cruises (Fig. 5). Of Rhodophyta, 5 taxa were restricted to the winter, 4

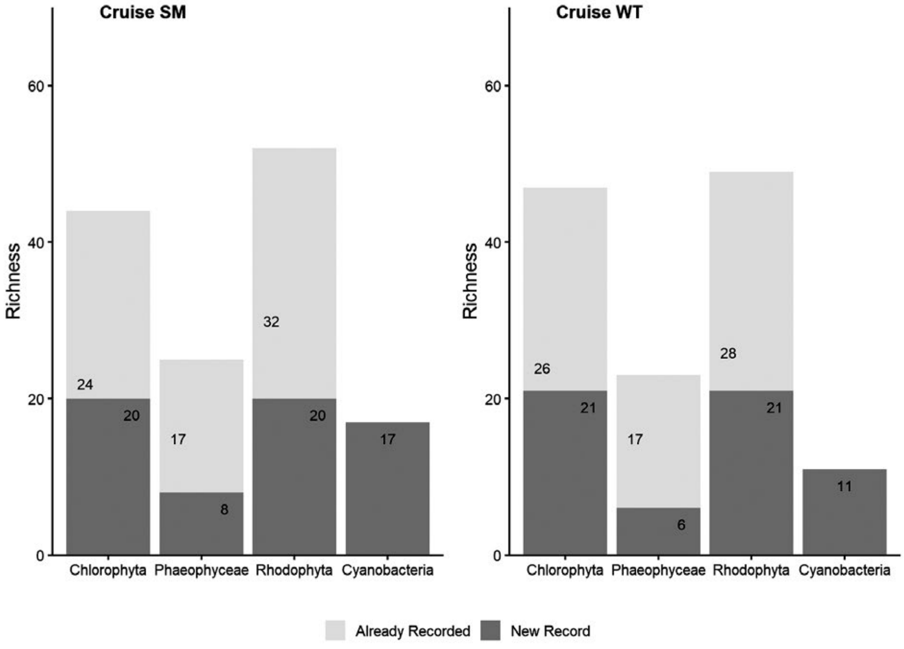

Fig. 5. – Temporal richness distribution of macroalgae groups and cyanobacteria from Trindade Island (southeastern Brazil, southwestern Atlantic), considering taxa already recorded (previous studies) and new records (present study) during summer and winter cruises (SM and WT, respectively).

were restricted to the summer and 16 were common to the summer and winter. Of Chlorophyta, 6 taxa were restricted to the winter, 4 were restricted to the summer, and 16 were common to the summer and winter. Finally, of Phaeophyceae, 1 species was restricted to the winter, 3 species were restricted to the summer, and 5 were common to the summer and winter.

Table 1 describes the presence (1) and absence (0) of new benthic macroalgae records from Trindade in summer and winter and the occurrence and habitat of each taxon along the southern (S) and northern (N) Trindade beaches: S (A, Andradas [20°30′37″S, 29°18′30″W]; T, Tartarugas [20°31′02″S 29°18′17″W]; P, Parcel [20°31′17″S 29°18′06″W]; PR, Príncipe [20°31′10″S 29°18′44″W]; L, Lixo [20°31′23″S 29°19′30″W]; F, Farilhões [20°31′32″S 29°19′49″W]); and N (E, Eme [20°30′49″S 29°20′22″W]; C, Calheta [20°30′29″S 29°18′41″W]; PO, Portugueses [20°30′21″S 29°19′01″W]; CA, Cabritas [20°29′38″S 29°19′51″W]; O, Orelhas [20°29′38″S 29°20′30″W]; PN, Ponta Norte [20°29′13″S 29°20′17″W]; N, Noroeste [20°30′18″S 29°20′36″W]). A comparative list of taxa occurrence is presented for the Brazilian coast, another Brazilian oceanic island and Caribbean, North Atlantic and South Atlantic Islands. In Table 1, a genus with no species ID refers to a genus that was not previously recorded for Trindade. In addition, a complementary checklist of species cited in previous studies and sampled in the present report is presented as supplementary material.

In general, considering the total richness and taxa diversity from Trindade, the most representative macroalgae group was Rhodophyta, represented by 24 families, dominated by Rhodomelaceae, Ceramiaceae and Corallinaceae. Calcareous, crustose, and branched specimens and conforming turf beds (tangled with Ceramiales and Bryopsidales, over-branched calcareous specimens) were dominant in Trindade. Rhodophyta was composed of 22% calcareous algae (Corallinaceae and Hapalidiaceae), forming rhodolith beds. Chlorophyta comprised 16 families, mainly dominated by Cladophoraceae, Caulerpaceae and Ulvaceae. Eleven families represented Phaeophyceae, with Dictyotaceae as the most representative (Supplementary material Fig. S1).

Cyanobacteria constituted 100% of the new records for the island and 13% of the total richness. Of these, 9 taxa were exclusive to the summer, 3 were exclusive to the winter, and 8 were common to both summer and winter (Supplementary material Table S1, Fig. 5). Filamentous cyanobacteria represented 11 families, dominated by Oscillatoriaceae and Nostocaceae.

Considering the total richness of Rhodophyta, Chlorophyta and Phaeophyceae, a cluster of similarity (Fig. 6) was formed with the populations from the south and north faces, showing ca. 78% similarity.

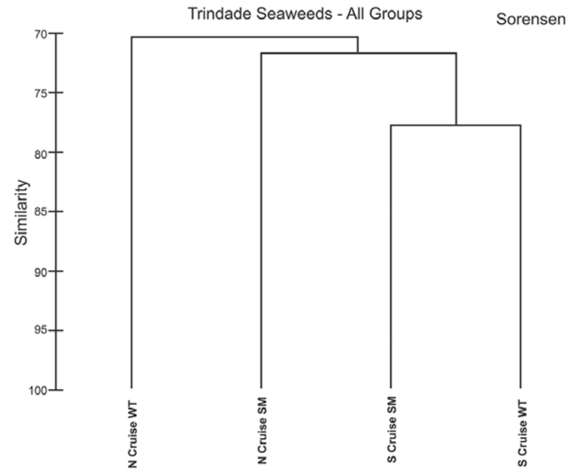

Fig. 6. – Sorensen similarity index considering macroalgae taxon richness (Rhodophyta, Phaeophyceae and Chlorophyta), comparing faces (N, north; S, south) and cruises (WT, winter; SM, summer) from Trindade Island.

Considering the abiotic data measured during the samplings (Table 2), higher temperatures salinities and UV max were recorded during the summer. The temperature ranges on the south face were 22.0±2.2°C and 27.5±2.0°C in winter and summer, respectively; those on the north face were 22.8±1.0°C to 27.8±1.0°C. The salinity on the south face ranged from 36.5±3.0 to 39.5±1.5 psu in winter and summer, respectively; that on the north face varied from 37.0±2.0 to 38.0±2.0. The pH showed higher values in summer (8.3±0.3) than in winter (8.2±0.5).

Minimum monthly rainfall values were recorded in spring/summer and maximum values in autumn/winter. UV radiation (more shaded) was 5±1 in winter and 8±2 in summer on the south face, compared with 6±1 in winter and 9±1 in summer on the north face. The seasonal differences between the north and south faces were not significant (p=0.74). Principal component analysis was performed using abiotic and richness data, but no exclusive factor was found to clearly influence the diversity.

DISCUSSION

New records, taxonomic status and perspectives

The mid- and shallow sublittoral zones and the algal turfs from Trindade Island had never been extensively and seasonally sampled before, and the present

Table 2. – Abiotic data (mean±SD) monitored *in situ* from Trindade Island (Southern Brazil, South-Western Atlantic), during the summer and winter cruises in 2014 and 2015, comparing the south and north faces.

Trindade island (BR)	South Summer/Autumn	South Winter/Spring	North Summer/Autumn	North Winter/Spring
Sea Surface Temperature (°C)	27.5±2	22±2.2	27.8±1	22.8±1
Salinity (psu)	39.5±1.5	36.5±3	38±2	37±2
pH	8.3±0.3	8.2±0.2	8.3±0.1	8.2±0.3
Wind Speed (km/h)	6±2	11±3	6±2	11±3
Precipitation (mm)	40±20	150±50	40±20	150±50
UV Max	8±2	5±1	9±1	6±1

study resulted in a significant increase in new records (approximately 35%). The greatest contribution is that of the 60 new records of seaweeds, representing an advancement in the understanding of Trindade macroalgae assemblages and suggesting the island as a candidate for a hotspot in the southwestern Atlantic (Table 1 and S1).

The present study recorded 141 species of macroalgae. According to Villaça et al. (2006), 13 taxa from the sublittoral zone (*Chaetomorpha nodosa* Kützing*, Codium decorticatum* Woodward*, Chamaedoris peniculum* (J. Ellis & Solander) Kuntze*, Siphonocladus tropicus* (P. Crouan & H. Crouan) J. Agardh*, Caulerpa mexicana* Sonder ex Kützing*, C. prolifera* (Roth) Kützing, *Avrainvillea nigricans* Decaisne*, Halimeda incrassata* (J. Ellis) J.V. Lamouroux, *Rhipilia sp., Arthrocardia flabellata* Kützing (Manza)*, Liagora ceranoides* J.V. Lamouroux*, Ceramium comptum* Borgesen*, Bryocladia thyrsigera* (J. Agardh) F. Schmitz) were not identified here. In addition, Pereira-Filho et al. (2011) added another 6 new occurrences to the list, also not recorded in our survey (*Champia parvula* (C. Agardh) Harvey*, Dasya brasiliensis* Oliveira Filho & Braga, *Heterosiphonia crassipes* (Harvey) Falkenberg*, Porolithon onkodes* (Heydrich) Foslie, *Phymatolithon masonianum* Wilks & Woelkerling*,* and *Spongites* sp.), the last three species being Corallinales, also from subtidal zone. Thus, the seaweed richness of Trindade comprises 160 species (Table S1, previous listed species). Reviewing the species found by previous studies but absent in ours, we may hypothesize some explanations: 1) the deeper subtidal was not our sampling zone focus; 2) some of these species may have been misidentified in the previous study; or 3) some species are becoming rare, with potential for local extinction.

Considering the last hypothesis, *Dasya brasiliensis*, an endemic species described from Brazil, had the last citation by Moura et al. (2015). *Bryocladia thyrsigera* and *Arthrocardia flabelatta* seem to be becoming rare. *B. thyrsigera,* an Atlantic species, was last listed in Brazil by Pellizzari et al. (2014), and *A. flabellata*, previously listed from South America and Africa, was last cited by Silva et al. (1996). Regarding *Spongites,* few valid species remain globally in the genus, and in Brazil the only record was for Trindade (Pereira-Filho et al. 2011). The other two Corallinales species mentioned were recently cited from Bahia, NE Brazil (Jesionek et al. 2016, Costa Jr. et al. 2002). Most of the green species mentioned are conspicuous in subtidal tropical and subtropical zones.

Climate change is inducing shifts in species ranges across the globe and monitoring them is crucial. Straub et al. (2019) argue that the "marine heatwaves" have been associated to changes in primary productivity, community composition and biogeography of seaweeds, which control ecosystem function and services. The authors compiled several observations related to resistance, bleaching, changes in abundance, species invasions and local to regional extinctions. More records existed for canopy-forming kelps, bladed and filamentous turf-forming seaweeds than for canopy-forming fucoids, geniculate coralline turf and crustose coralline algae. Turf-forming seaweeds, especially invasive seaweeds, generally increased in abundance after a marine heat wave, whereas native canopy-forming typically declined in abundance. In contrast, Buonomo et al. (2018) announced the predicted extinction of unique genetic diversity in marine forests of *Cystoseira* spp. in the Mediterranean Sea, whose habitats are becoming more limited. Thomsen et al. (2019) also report local extinction of bull kelp (*Durvillaea* spp.) due to a marine heatwaves.

Marine vegetational habitats are the most sensitive descriptors for assessing environmental changes. Porzio and Buia (2020) detected a severe loss of Fucales and seagrass meadows in the Gulf of Pozzuoli (Italy), demonstrating that human-made coastline seems to be the leading cause of vegetational habitat regression. Gorman et al. (2019) report decadal losses of canopy-forming algae along 1000 km of Brazilian coast, using meta-analysis to examine long-term changes (a time span of 48 years) in the cover and biomass of *Sargassum* spp. The authors revealed major declines independent of seasons, suggesting overall losses of 52%, particularly at sites exhibiting the greatest degree of coastal warming and the highest population and those located in semi-enclosed sheltered bays. In addition, the authors also observed enhance of turf-forming assemblages (filamentous and articulated coralline).

In contrast to data reported for other global coastal areas, species rarity, reduction and replacement of biomass, local extinctions or the predominance/substitution of specific groups of macroalgae has not yet been observed in Trindade, a remote and uninhabited island. Coastal and insular ecosystems show different mechanisms for responding to impacts, mainly because in insular oceanic areas turf forms the main natural assemblages due to oligotrophic conditions, and its biomass is not a suitable indicator of changes in these areas, particularly if it is used isolated. However, because of lower direct anthropogenic impacts they suffer, remote islands are key indicators of meteorological and oceanographic changes.

The higher richness observed in our study, compared with previous ones (summarized in Villaça et al. 2006), is primarily associated with our sampling effort focused along the intertidal and shallow subtidal zones (different from previous studies); and for the fact that our data were obtained seasonally on several Trindade beaches, being the first spatio-temporal assessment for the island. Previous studies obtained mainly dredged samples from greater depths, which is a destructive method and may have resulted in underestimated results and in an unspecified area (Pedrini et al. 1989, Yoneshigue-Valentin et al. 2005).

The low standardization and randomness of the past samplings may have played a role in the observation of higher richness in this study. In addition, the majority of the new records were small and inconspicuous specimens from algal turf, whose presence may have gone unnoticed until the current implementation of large-scale sampling.

Molecular data are essential for current taxonomical approaches, especially for cryptic seaweed species (including cyanobacteria), and their lack may lead to an underestimation of species richness. However, in some specific cases such as the present study, classical morphological taxonomy may not be considered an inconsistent tool, particularly due to the difficulty of isolating sufficient unialgal material from the entangled turf assemblage in a low-resource laboratory on the island (Fig. 3). Furthermore, a posteriori in vitro culture of the target specimens on return from the island would be necessary to obtain sufficient cryptic material for molecular analysis. However, cryptic species culture is not always successful and may represent difficulties in studying turf assemblages. As an example of current diversity issues, *Hildenbrandia rubra* has over 70 genetic groups sampled in the Northern Hemisphere attributable to this morphological species (Mathieson and Dawes 2017). The morphological identities are a conundrum, even to taxonomic experts who grasp what species are present and taxonomically valid. However, the focus on non-conspicuous or cryptic species is due to several introduction events and the progression of the exogenous species, which has thus far been undetected owing to its morphological similarities with conspicuous and native species. For this reason, continuous monitoring is fundamental, and classic morphological-assisted studies are essential because of their low cost, particularly where higher richness is prevalent, and because of the difficulty of sampling monospecific specimens from complex macroalgae assemblages such as turfs. Moreover, only a few groups of global diversity are considered cryptic and should be the target of molecular studies, providing reliability and satisfying the demand for morphological identification.

The richness of Chlorophyta in Trindade surpasses that of any other oceanic island in the Atlantic. In the present survey, 9 species of *Cladophora* were identified. Miranda-Alves (2015) identified 22 Cladophoraceae species in the coast of Brazil, 19 species of *Cladophora* and 3 species of *Willeella*. This molecular study identified new records that need to be described: *C. coelothrix* of Brazil (nom. prov.) and *C. laetevirens* of Brazil (nom. prov.), *C. prolifera* of Brazil (nom. prov.), *C. rupestris* of Brazil (nom. prov.), and another 3 species of *Cladophora* (named sp. 2 to sp. 4). The author mentions that morphological characteristics confirmed only five species on the Brazilian coast: *C. brasiliana, C. corallicola, C. sericea, C. socialis*, and *C. vagabunda*. Based on these results, the need for further molecular studies to better understand the phylogenetic relationships of the group became evident. Our research team is currently studying cryptic Chlorophyta from the southern Atlantic oceanic islands in detail.

Specimens of Prasiolales were also identified in Trindade. Although its distribution is concentrated in temperate and polar eutrophic waters, and it is considered cryptic, *Prasiola* sp. associated with other benthic macroalgae in salt lagoons from Venice (Italy, Mediterranean Sea) was reported to occur by Miotti et al. (2005). This suggests the need for a molecular investigation of this group in the Atlantic Ocean islands, owing to the possibility of geographical distribution expansion to warmer areas and/or introduction. Cryptic species among seaweed groups have been reported in several molecular studies: *Hesperophycus* and *Pelvetiopsis* (Neiva et al. 2017); *Colpomenia sinuosa* (Lee et al. 2013); and *Polysiphonia morrowii* (Geoffroy et al. 2012). In addition, Saunders et al. (2019), using a DNA barcode, studied Rhodophyta diversity from Tristan da Cunha. *Ceramium secundatum, Colaconema caespitosum, Helminthocladia calvadosii* and *Porphyra mumfordii* were suggested as species that increased their biogeographic distribution, probably because of human activity.

Halymenia vinacea and *Grateloupia* cf. *filicina* are also new records for Trindade. Azevedo (2016), studying the phylogeny of Halymeniales from the Brazilian coast, stated that the taxonomy of the group is problematic, possibly including misidentifications. The author demonstrated the existence of wide cryptic and pseudo-cryptic diversity, as well as novel species and genera, and revealed the presence of non-native Rhodophyta. The rare and delicate new turf records of *Melanothamnus tongatensis, Polysiphonia sertularioides* and *Vertebrata foetidissima* are not just limited to the Brazilian coast but occur widely in the Canary, Azores and Cape Verde islands and in the Caribbean Sea, which also suggests the extension of their geographical distribution to Trindade.

Oliveira et al. (2009) listed the new occurrence of *Blidingia marginata*, *Halimeda gracilis*, *Dictyota caribaea* and *Sargassum hystrix var. buxifolium* to Fernando de Noronha Archipelago, which not only represents new additions to the area but also demonstrates a geographical distribution extension of the species to the tropical SW Atlantic Ocean.

Only a single species of *Sargassum* was recorded to Trindade, *S. vulgare v. nanum,* not conspicuous on the island. The lack of other Fucales and the common presence of Dictyotales coincide with a recent massive dispersion of benthic algae off Trindade and on the Brazilian coast. According to Sissini et al. (2017b), the floating *Sargassum* biomass that reached the northern Brazilian coast and Fernando de Noronha archipelago in 2014 and 2015 (peaking 98 kg m^{-2} wet weight) was molecularly identified as *Sargassum natans* and *S. fluitans.* Satellite images did not support the hypothesis of slicks moving south from the Sargasso Sea (northern Atlantic Ocean). The author discussed that there is probably a matrix of holopelagic *Sargassum* in the central Atlantic Ocean, and biomass accumulation should be considered the result of the combination of physico-chemical seawater conditions and biological interactions, as well as environmental stress. Meanwhile, these floating islands are a fundamental element of the biogeography and macroecology of tropical environments, which may provide connectivity among the marine biodiversity from Atlantic reef environments by transporting associated phycoflora and fauna to other areas, including remote islands.

Regarding cyanobacteria, in Brazil, there is only one thesis published specifically for marine filamentous cyanobacteria (Crispino 2007), with sporadic references to the Noronha and Abrolhos archipelagos. In this study, which presents the first checklist for remote areas in the southern Atlantic, 20 taxa (9 genera and 11 species) of filamentous cyanobacteria were identified permeating the turf. These organisms inhabit diversified and extreme environments and may indicate environmental changes (Crispino and Sant'Anna 2006). Following Sangil et al. (2012), cyanobacteria can be opportunistic where seawater warming has taken place, and a higher biomass of cyanobacteria was also documented in the shallow waters of Puerto Rico, Caribbean Sea (Stielow and Ballantine 2003).

Considering the new seaweed records for Trindade and the establishment of an updated taxonomic database, this study recommends possible cryptic groups as the target for further molecular studies aiming to elucidate new trends in macroalgae dispersion patterns due to thermohaline and ocean current changes.

Higher richness *vs.* abiotic changes: bridging or introductions?

An increase in the area of biogeographic distribution of a given species and new occurrences of species or algal groups that had not previously been reported for a given area have been largely associated with the current environmental changes. There is a large focus on the effects of higher SST and concurrent distributional shifts of seaweed assemblages, and several studies suggest large-scale meteorological and oceanographic changes as a potential driver of biota changes (Sangil et al. 2010, Clemente et al. 2011, Pellizzari et al. 2017).

The local abiotic data sampled in Trindade Island are not sufficient to support short-term thermohaline changes (Table 2) or significant differences between data from the south and north faces of the island. However, on the basis of historical data (Fig. 2), temperature and salinity seem to be dynamic parameters in the surroundings of Trindade. These trends may be consequences of a complex oceanic circulation in the area (Fig. 1), but it is also noteworthy that recent thermohaline anomalies (2017) might have long-term effects on the seaweed assemblages in Trindade.

Our data showed a high Chlorophyta richness among the southern Atlantic islands. This opportunistic group deserves attention as a bioindicator of changes. Similarly, Afonso-Carrillo et al. (2007) reported that a subtidal algae bed in the Canary Islands has undergone changes, indicated by the proliferation of the ephemeral green algae *Pseudotetraspora marina*, a recent and probably introduced species reported for the eastern Atlantic Ocean. Sangil et al. (2012) associated the shifts in the distribution and biomass of ephemeral species with the 2°C warming in the SST resulting from the weakening of the cold Canary current.

In addition, some new records listed in Trindade include potential cryptogenic species (of unknown origin), such as *Feldmannia indica*, *Dictyota jamaicensis*, *Melanothamnus tongatensis* and *Parviphycus trinitatensis*. Meanwhile, *F. indica* is widespread in warmer seas (Guiry and Guiry 2020) and, according to Tronholm et al. (2013), *Dictyota jamaicensis* has been reinstated as an amphi-Atlantic species (Caribbean-Brazil-Cape Verde/Africa), suggesting that the new record for Trindade may also "bridge" this distribution.

Overall, a greater similarity of Trindade seaweed assemblages (Table 3) to phycoflora of Ascension (Tsiamis et al. 2014) and to those of other Brazilian oceanic islands, i.e. those between latitudes 27-29°N and 20-21°S, was observed. Some similarities to assemblages from areas of higher latitudes in the Northern Hemisphere (such as the Azores and Cape Verde islands) were also observed. However, poor similarity to assemblages from islands of the Southern Hemisphere (Gough and Tristan da Cunha) was observed. Despite the need for confirmation by population and biogeographic genetics studies, the thesis that Trindade seaweed diversity has been irradiated from the Caribbean Sea is supported. In addition, considering the current environmental changes, the connectivity between these areas previously considered remote is increasing.

In addition to temperature and salinity, pH values were the abiotic data that most differed from the standard values for the surroundings of Trindade (expected range, 8.05-8.10; data source, research.noaa.gov/acidification). The observed pH was constant and homogeneous throughout Trindade (approximately 8.3), although higher than the expected range. Trindade exhibits high seaweed richness, but few species contribute to the total coverage. In some oceanic islands, rhodoliths and crustose calcareous algae may reach a biomass of approximately 70% (Brasileiro et al. 2016). The higher pH observed is probably related to the dominance of calcareous specimens, which may form

Table 3. – Comparison of studies from the southern Atlantic oceanic islands, considering macroalgae richness by groups (Rhodophyta, Phaeophyceae and Chlorophyta).

Oceanic Islands, Southern Ocean	Rhodophyta	Phaeophyceae	Chlorophyta	References
Trindade (mid- and upper sublittoral)	58	28	55	This study
Trindade (sublittoral up to 50 m, dredged/diving specimens)	55	21	47	Pedrini et al. (1989), Nassar (1994), Yoneshigue-Valentin et al. (2005), Villaça et al. (2006)
Atol das Rocas	53	28	23	Oliveira and Ugadim 1976, Villaça et al. (2010)
Fernando de Noronha archipelago	86	28	54	Pedrini et al. (1992), Pereira-Filho et al. (2015), Amado-Filho et al. (2012), Burgos (2011)
São Pedro e São Paulo archipelago	24	8	11	Burgos et al. (2009), Villaça et al. (2006)
Ascension Island (UK, outgroup)	75	15	23	Tsiamis et al. (2014)

an 'alkaline ring' surrounding the island, a biopredictor that can be interpreted as a positive anomaly in contrast with global trends of acidification and deserves further investigation.

Articulated calcareous algae (e.g. *Jania* and *Amphiroa* spp.) at Trindade constitute algae 'turf' mats, often the primary coverage of benthic biogenic oligotrophic habitats. In addition, calcareous crustose and rhodoliths establish extensive beds at the island. According to Sissini (2013), its calcareous algae are dominated by *Mesophyllum erubescens*, *M. engelhartii*, *Mesophyllum* sp. and *Lithothamnion* sp. Two new putative species are under investigation using molecular markers. Corallinaceae are among the oldest known rhodophyte fossils, and it would be surprising to find endemic species in Trindade in this family, particularly because of the relatively recent volcanic events at the island. In this survey, 3 encrusting species were identified and 10 were articulated. However, the identification of corallines from Brazil (*Mesophyllum* species in particular) is indeed in a poor state. *Lithophyllum (Titanoderma) prototypum* was identified at Trindade and also reported for Abrolhos Bank (Jesionek et al. 2016). This species is not conspicuous at Trindade; it is restricted to a depth of 2-10 m and is generally sampled as a non-fertile single specimen. Further investigation is needed to solve this taxonomic impasse.

The seaweed richness of Trindade was underestimated, and the distributional limits of some new records are probably shifting, highlighting the importance of long-term monitoring of the Brazilian oceanic islands. The spatio-temporal differences and high richness of cyanobacteria and Chlorophyta demand further investigation to establish phylogenetic relationships and detailed correlations with the abiotic oscillations. In addition, the richness enhancement of a given group of organisms may appear at a first glance to be a positive aspect, but it may also be an indicator of change in an area with biogeographical isolation, especially when it is accompanied by low endemism.

Connectivity and low endemism: facing current environmental trends

The present data were permeated by the low endemism of seaweeds at Trindade Island. The interaction of distinct water masses (Fig. 1) results in a complex mosaic of physical and chemical seawater conditions, featuring the co-occurrence of tropical, subtropical and warm-temperate species. These data may also corroborate Trindade's geological data. Pires et al. (2016) report that the last volcanic phase occurred in post-glacial times, which would indicate the last activity to have occurred approximately 25000 years ago. These data may justify the low endemism reported in the phycoflora from Trindade, suggesting that the organisms may have successfully dispersed to Trindade and to Brazil from the Caribbean.

Biogeographic island models have emerged from the study of terrestrial organisms. Considering oceanic ecosystems, seaweeds may expand their distribution using "stepping-stones" and currents, with abiotic features similar to their origins providing more possibilities for speciation (Pinheiro et al. 2017). Remote islands are natural laboratories for elucidating biotic changes. This list of new macroalgae records suggests that marine ecosystems respond to isolation differently than terrestrial organisms. The distribution of Trindade assemblages seems to reflect the complex circulation of the Subtropical Gyre, receiving influences from the Brazil, South Atlantic, and South Equatorial currents and vortices from the Agulhas Current and the Angola-Benguela Front (Sissini et al. 2017a). Meanwhile, Trindade has been described as an ecotone (Horta et al. 2001), i.e. a transition area that, in theory, limits the beginning and end of populations of different origins. Our data suggest Trindade is a 'transit' zone, where low endemism may be a result of complex connectivity relationships. Moreover, this species transit is corroborated by algal species that are expanding their distribution limits from these areas previously considered "isolated".

In recent decades, climate change has caused profound biological changes across the planet. However, there is a large disparity of data between hemispheres and a scarcity of studies using seaweeds as proxies (Pellizzari et al. 2017, Santos-Silva et al. 2018). Sorte et al. (2010), Hoegh-Guldberg and Bruno (2010), and Wernberg et al. (2011a, b) showed evidence of the rearrangement of entire communities rather than mere changes in individual species. Seaweed population changes can have severe impacts on the entire food web, and for this reason there is a major challenge in interpreting the results, including our data.

As summarized by Jueterbock et al. (2013), environmental changes may cause several impacts on seaweed populations: 1) distributional shifts; 2) higher herbivory pressure; 3) higher phenotypic plasticity and adaptive responses due to thermal change; 4) higher competitive interactions and habitat loss; and 5) changes in dispersion patterns and greater invasive potential. As already discussed by Pellizzari et al. (2017) and Sanches et al. (2016) for Antarctic islands, it is possible that Trindade is also experiencing changes in macroalgal richness and distribution because of a new trend towards higher connectivity of areas previously considered biogeographically isolated. This study listed new records of non-endemic (including cryptic and cryptogenic) species, drawing attention to the effects of current abiotic changes and proposing an updated taxonomic baseline for future comparative studies in tropical areas.

According to Straub et al. (2019), although a relatively small number of studies have described impacts of marine heat waves on seaweed, the broad range of documented responses highlights the necessity of better baseline information regarding seaweed distributions and performance, and the need to study specific parameters that affect the vulnerability and resilience of seaweeds to these increasing climatic perturbations. A major challenge will be to disentangle impacts from co-occurring potential stressors, including altered current patterns, increasing herbivory, changes in transparency and nutrient concentration, solar radiation and desiccation stress in the intertidal zone.

Trindade is an oceanic island that has the potential to facilitate the treatment of important biological issues. Further studies establishing a baseline for species diversity using molecular data would confirm information on new biogeographic issues facing current environmental changes. Moreover, several putative invasive species could also be confirmed. Considering that some regions of the islands are geologically young, endemism may also have been underestimated. Finally, Trindade may be an interesting model for studying transoceanic re-colonization pathways.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available through the online version of this article and at the following link: http://scimar.icm.csic.es/scimar/supplm/sm05036esm.pdf

Table S1. – List of seaweed species already reported from Trindade Island, southwestern Atlantic, complementary to the new occurrences recorded in the present study.

Fig. S1. – Larger and conspicuous seaweeds that grow on top of the turf and rhodolith beds along the midlittoral and shallow sublittoral (A, Dictyotales; B, *Caulerpa verticillata*; C, Tribe Laurencieae). Scale = 1 cm.

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New records of seaweeds and filamentous cyanobacteria from Trindade Island: an updated checklist to support conservation guidelines and monitoring of environmental changes in the southern Atlantic archipelagos

Franciane Pellizzari, Vanessa Sayuri Osaki, Michelle C. Santos-Silva

Supplementary material

Table S1. – List of seaweed species already reported from Trindade Island, southwestern Atlantic, complementary to the new occurrences recorded in the present study.

CHLOROPHYTA
Acetabularia sp.
Anadyomene saldanhae A.B.Joly & E.C.Oliveira
Anadyomene stellata (Wulfen) C.Agardh
Boodleopsis pusilla (Collins) W.R.Taylor, A.B.Joly & Bernatowicz
Bryopsis pennata J.V.Lamouroux
Bryopsis plumosa (Hudson) C.Agardh
Caulerpa ambigua Okamura
Caulerpa fastigiata Montagne
Caulerpa racemosa (Forsskål) J.Agardh
Caulerpa verticillata J.Agardh
Caulerpa webbiana Montagne
Chaetomorpha aerea (Dillwyn) Kützing
Chaetomorpha antennina (Bory) Kützing
Chaetomorpha sp.
Cladophoropsis membranacea (Hofman Bang ex C.Agardh) Børgesen
Dasycladus vermicularis (Scopoli) Krasser
Dictyosphaeria cavernosa (Forsskål) Børgesen
Dictyosphaeria ocellata (M.Howe) Olsen-Stojkovich
Dictyosphaeria versluysii Weber-van Bosse
Halimeda discoidea Decaisne
Halimeda tuna (J.Ellis & Solander) J.V.Lamouroux
Neomeris annulata Dickie
Penicillus capitatus Lamarck
Phyllodictyon anastomosans (Harvey) Kraft & M.J.Wynne
Udotea flabellum (J.Ellis & Solander) M.Howe
Ulva lactuca Linnaeus
Ulvella lens P.Crouan & H.Crouan
Valonia utricularis (Roth) C.Agardh
Willeella brachyclados (Montagne) = *Cladophora montagneana*
PHAEOPHYCEAE
Asteronema breviarticulatum (J.Agardh) Ouriques & Bouzon
Bachelotia antillarum (Grunow) Gerloff
Chnoospora minima (Hering) Papenfuss
Colpomenia sinuosa (Mertens ex Roth) Derbès & Solier in Castagne
Canistrocarpus cervicornis (Kützing) De Paula & De Clerck
Dictyopteris delicatula J.V.Lamouroux
Dictyopteris plagiogramma (Montagne) Vickers
Dictyota bartayresiana J.V.Lamouroux
Dictyota menstrualis (Hoyt) Schnetter, Hörning & Weber-Peukert
Dictyota mertensii (C.Martius) Kützing
Feldmannia irregularis (Kützing) Hamel
Feldmannia mitchelliae (Harvey) H.-S.Kim
Lobophora variegata (J.V.Lamouroux) Womersley ex E.C.Oliveira
Neoralfsia expansa (J.Agardh) P.-E.Lim & H.Kawai ex Cormaci & G.Furnari
Padina gymnospora (Kützing) Sonder
Padina sanctae-crucis Børgesen
Sargassum vulgare var. nanum E.de Paula
Sphacelaria rigidula Kützing
Sphacelaria tribuloides Meneghini
RHODOPHYTA
Acrochaetium microscopicum (Nägeli ex Kützing) Nägeli
Aglaothamnion uruguayense (Taylor) Aponte, Ballantine & Norris
Amphiroa fragilissima (Linnaeus) J.V.Lamouroux
Botryocladia pyriformis (Børgesen) Kylin
Centroceras clavulatum (C.Agardh) Montagne
Ceramium brasiliense A.B.Joly
Ceramium dawsonii A.B.Joly
Ceratodictyon variabile (J.Agardh) R.E.Norris
Chondria polyrhiza Collins & Hervey
Digenea simplex (Wulfen) C.Agardh
Erythrotrichia carnea (Dillwyn) J.Agardh
Gayliella flaccida (Harvey ex Kützing) T.O.Cho & L.J.McIvor
Gelidium pusillum (Stackhouse) Le Jolis
Gracilaria cornea J.Agardh
Gymnothamnion elegans (Schousboe ex C.Agardh) J.Agardh
Herposiphonia secunda (C.Agardh) Ambronn
Herposiphonia tenella (C.Agardh) Ambronn
Heterosiphonia crispella (C.Agardh) M.J.Wynne
Hypnea spinella (C.Agardh) Kützing
Jania adhaerens J.V.Lamouroux
Jania cubensis Montagne ex Kützing
Jania rubens (Linnaeus) J.V.Lamouroux
Leptofauchea rhodymenioides W.R.Taylor
Melanothamnus ferulaceus (Suhr ex J.Agardh) Díaz-Tapia & Maggs
Melanothamnus harveyi (Bailey) Díaz-Tapia & Maggs
Ophidocladus simpliciusculus (P.Crouan & H.Crouan) Falkenberg
*Palisada flagellifer*a (J.Agardh) K.W.Nam
Parviphycus trinitatensis (W.R.Taylor) M.J.Wynne
Polysiphonia howei Hollenberg
Polysiphonia subtilissima Montagne
*Sahlingia subintegr*a Cocks ex Bornet
Taenioma nanum (Kützing) Papenfuss
Tricleocarpa fragilis (Linnaeus) Huisman & R.A.Townsend

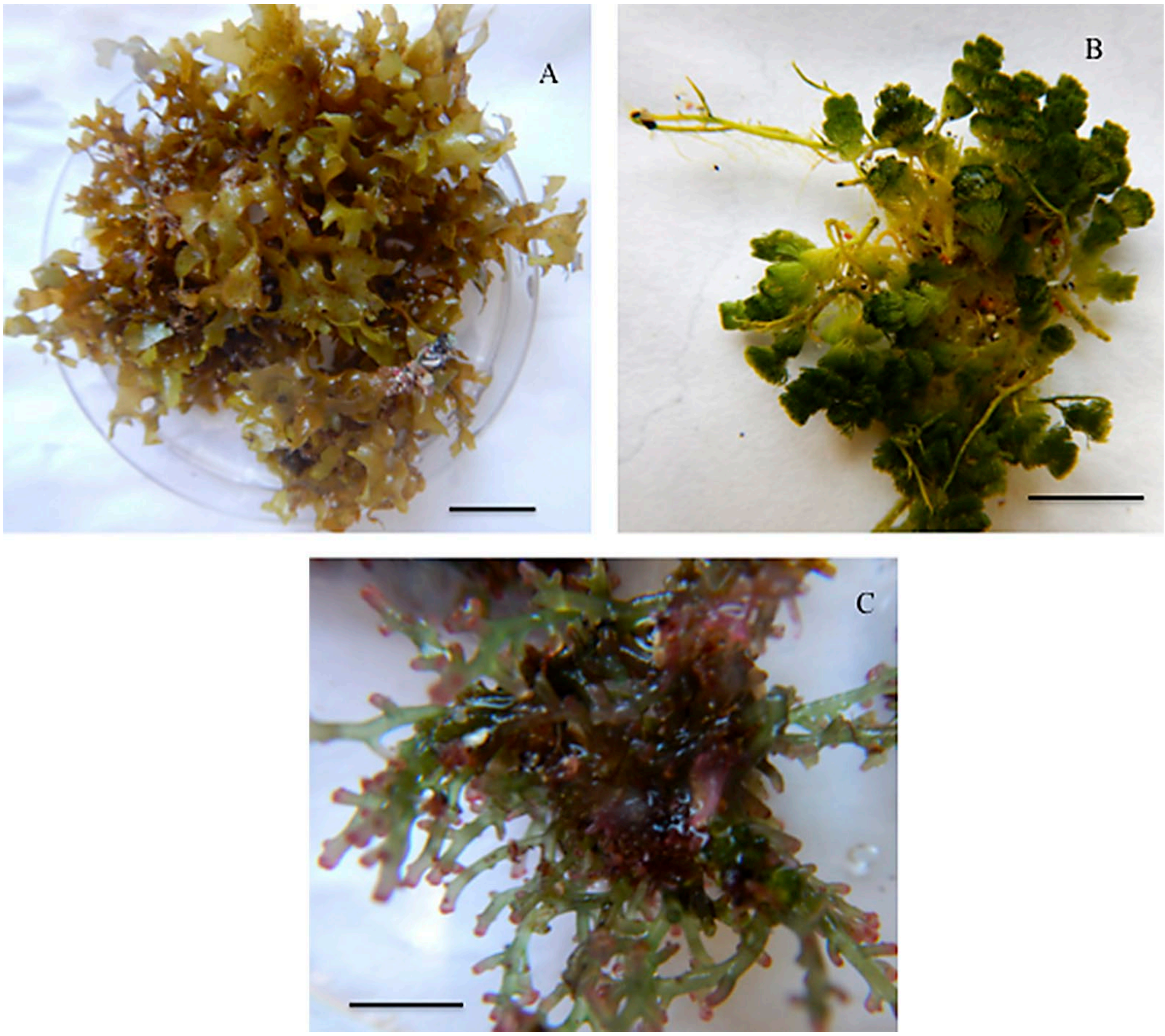

Fig. S1. – Larger and conspicuous seaweeds that grow on top of the turf and rhodolith beds along the midlittoral and shallow sublittoral (A, Dictyotales; B, *Caulerpa verticillata*; C, Tribe Laurencieae). Scale = 1 cm.