Polar Biology (2023) 46:489–496
https://doi.org/10.1007/s00300-023-03136-6

BRIEF REPORT

The first record of a non-native seaweed from South Georgia and confirmation of its establishment in the Falkland Islands: *Ulva fenestrata* Postels & Ruprecht

Robert J. Mrowicki[1] · **Juliet Brodie**[1]

Received: 22 December 2022 / Revised: 20 March 2023 / Accepted: 4 April 2023 / Published online: 26 April 2023
© The Author(s) 2023

Abstract
Detecting non-native species can be challenging, particularly in the case of taxa such as seaweeds, which can be difficult to distinguish based on morphology and often require molecular-assisted taxonomy for reliable identification. The sub-Antarctic island of South Georgia supports unique and important marine biodiversity, including a rich seaweed flora, but despite its isolation, its inshore ecosystems are susceptible to the introduction of potentially invasive non-native species. Here, we provide the first report of a non-native seaweed in South Georgia, *Ulva fenestrata* Postels & Ruprecht (Ulvophyceae, Chlorophyta), and confirm its widespread presence in the Falkland Islands via molecular-assisted taxonomy. Phylogenetic analyses of *tufA* and *rbc*L-3P genetic markers enabled the identification of a specimen collected from Grytviken, South Georgia in November 2021 as *U. fenestrata*. In terms of *tufA* sequence, this sample was identical to specimens collected from four sites spanning West and East Falkland in 2013 and 2018. This study represents the second Southern Hemisphere record of *U. fenestrata*, which is generally regarded as a Northern Hemisphere species. Our findings provide a foundation for monitoring this potentially invasive species in South Georgia, and for determining its likely source and mode of arrival, while emphasising the importance of robust biosecurity measures.

Keywords Chlorophyta · DNA barcoding · Marine biodiversity · *rbc*L-3P · Sub-Antarctic · *tufA*

Introduction

The rate of detection of non-native species in aquatic ecosystems worldwide has increased substantially over recent decades, with seaweeds (marine macroalgae) accounting for over 14% of detected introductions (Bailey et al. 2020). Although the number of known non-native seaweed species has increased in recent years (Williams and Smith 2007; Thomsen et al. 2016a; Costello et al. 2021), this probably represents an underestimate, owing to undetected introductions and a lack of taxonomic information (Bailey et al. 2020). Non-native seaweeds have potentially pervasive impacts on marine biodiversity and ecosystem functioning, typically exerting negative effects on the abundance and diversity of native biota (Williams and Smith 2007; Thomsen et al. 2016a), yet their effects are context dependent, with the potential to be exacerbated by climate change and other environmental stressors (Bax et al. 2002; Thomsen et al. 2016b; Bennett et al. 2021). Similarly, the "invasion success" of a particular non-native seaweed is difficult to predict, depending on the attributes of both the non-native species and the invaded ecosystem and, perhaps less importantly, the lack of coevolution with native species (Thomsen et al. 2016a).

In order to detect and monitor the arrival, distribution and impact of non-native seaweeds effectively, it is essential that species are reliably identified. Certain groups of seaweeds are notoriously difficult to distinguish based on morphology alone and require molecular-assisted taxonomy for accurate identification (Saunders and Kucera 2010; Tran et al. 2022). DNA-barcoding studies of morphologically indistinct and phenotypically variable taxa, such as foliose green seaweeds of the cosmopolitan genus *Ulva*, have revealed cryptic diversity and confirmed the presence of non-native species in many parts of the world (e.g. Heesch et al. 2009; Krupnik et al. 2018; Wei et al. 2022). In addition, the family

✉ Juliet Brodie
j.brodie@nhm.ac.uk

[1] Natural History Museum, Cromwell Road, London SW7 5BD, UK

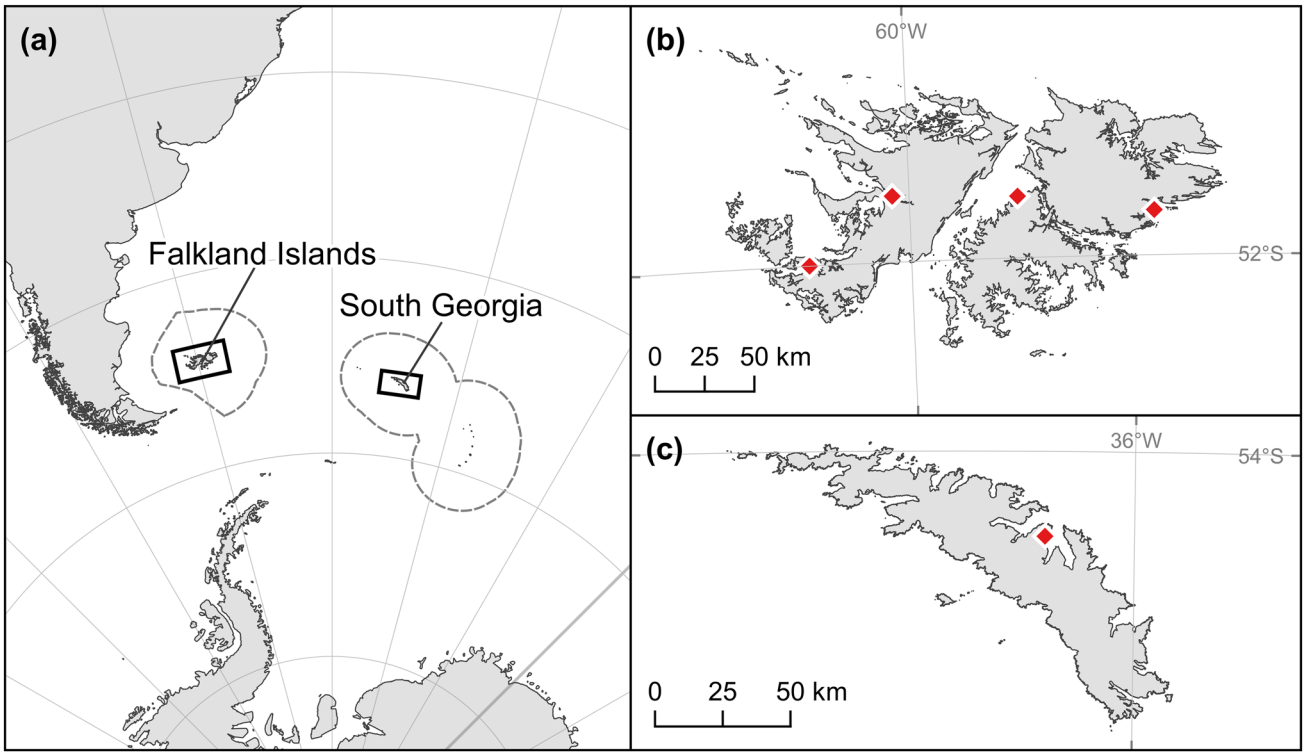


Fig. 1 **a** The locations of the Falkland Islands and South Georgia in the southwest Atlantic Ocean (dashed lines represent the respective Exclusive Economic Zone boundaries), and collecting sites for *Ulva fenestrata* in (**b**) the Falkland Islands and **c** South Georgia

Ulvaceae, to which this genus belongs, includes a disproportionately high number of known non-native species, and is regarded as a group with a great proclivity for invasion (Williams and Smith 2007). The use of a robust taxonomic approach for enhancing our knowledge of seaweed biodiversity is particularly important in remote areas where invasive species pose a significant threat to marine ecosystems comprising a relatively high proportion of rare and/or endemic species (Clubbe et al. 2020; Dawson et al. 2022), especially given the greater tendency for non-native seaweeds to exert negative effects on native biota in relatively pristine environments (Thomsen et al. 2016a).

The remote sub-Antarctic island of South Georgia supports a rich seaweed flora (John et al. 1994; Wells et al. 2011; Mrowicki and Brodie, pers. obs.), although its shallow subtidal ecosystems remain poorly studied (Barnes et al. 2006; Rogers et al. 2015), particularly with regard to seaweeds (Clubbe et al. 2020). Existing seaweed species lists for South Georgia are based on morphological identification and outdated species concepts, making it difficult to make biogeographical comparisons; however, given the dominance of endemic and range-edge species in South Georgia's benthic invertebrate fauna (Hogg et al. 2011), its seaweed flora may be expected to have similar characteristics. The unique inshore marine biodiversity of South Georgia faces threats predominantly from climate change and invasive species (Hogg et al. 2011; Rogers et al. 2015), including seaweeds, which could be introduced to the island via international shipping (Dawson et al. 2022) involving tourist, research and fishing vessels. Many of these vessels arrive from the Falkland Islands, located approximately 1450 km west of South Georgia, which, therefore, represent a potential source of marine non-natives. While it is estimated that non-native species account for 70% of the island's terrestrial flora (Clubbe et al. 2020), there have been no confirmed reports of non-native seaweeds in South Georgia, despite a number of species having been identified as high risk in terms of their likely arrival, establishment and ecological impact (Dawson et al. 2022). Here, we provide the first record of a non-native seaweed in South Georgia, *Ulva fenestrata*, and evidence of its establishment in the Falkland Islands, supported by molecular-assisted taxonomy.

Methods

Specimen collection

Seaweed specimens were collected from the shallow sublittoral zone at Grytviken, South Georgia (14th November 2021) and from the intertidal zone at four sites in the Falkland Islands (December 2013–February 2018; Figs. 1 and

2; Online Resource 1). Tissue samples for DNA extraction (~0.1 cm^2 with no visible epiphytes) were either dissected from fresh material and preserved in silica gel in the field (South Georgia) or removed from dried herbarium specimens (Falkland Islands). All material is housed in the algal herbarium at the Natural History Museum, London, UK (BM).

DNA sequencing

DNA extraction, amplification and sequencing methods are described in Brodie et al. (2021). Two plastid markers were sequenced: for all specimens, (1) an 855 bp region of the translation elongation factor Tu (*tufA*), using primers tufGF4 (Saunders and Kucera 2010) and tufAR (Famà et al. 2002); and, for the South Georgia specimen only, (2) the 742 bp 5′ end of the rubisco large subunit (*rbc*L-3P), using primers GrbcLFi (Saunders and Kucera 2010) and 1385R (Manhart 1994). PCR thermal profiles for *tufA* and *rbc*L-3P followed Saunders and Kucera (2010). Sanger sequencing was performed at the Natural History Museum using a 3730xl DNA Analyzer (Applied Biosystems, USA).

Data analyses

Forward and reverse sequences were aligned, edited and trimmed using Unipro UGENE (v40.0; Okonechnikov et al. 2012). Additional sequences were obtained from GenBank and added to *tufA* and *rbc*L-3P datasets, including three outgroup sequences per dataset (Online Resource 2). Resulting *tufA* ($n=24$) and *rbc*L-3P ($n=26$) were aligned separately using MAFFT (v7.505; Katoh and Standley 2013) via the L-INS-I algorithm. Prior to phylogenetic analyses, regions of poor alignment and sites containing gaps were removed from each alignment using Gblocks (v0.91b; Castresana 2000), resulting in 674 and 621 sites for *tufA* and *rbc*L-3P, respectively. Analyses were performed on both single-marker alignments separately, in addition to a concatenated alignment (*tufA* + *rbc*L-3P) including 18 sequences (total 1295 sites). Best-fit partitioning schemes and corresponding nucleotide substitution models, based on the corrected Akaike Information Criterion (AICc), were determined for all three alignments using PartitionFinder (v2.1.1; Lanfear et al. 2016; Online Resource 3).

Phylogenetic relationships were inferred based on Bayesian and maximum likelihood optimality criteria, using MrBayes (v3.2.6; Ronquist et al. 2012) and RAxML-NG (v1.1.0; Kozlov et al. 2019), respectively. Bayesian analysis was performed using two runs of four Markov chains over 5 million generations, sampling every 100 generations, with the first 25% of trees discarded as "burnin". Convergence was diagnosed using the average standard deviation of split frequencies (ASDSF; $\ll 0.01$) in addition to potential scale reduction factors (PSRF; ≈ 1) and estimated sample sizes (ESS; > 200) for all parameters, and by examining parameter log-likelihood traces using Tracer (v1.7.1; Rambaut et al. 2018). Maximum likelihood analysis involved 100 tree searches using 50 random and 50 parsimony-based starting trees, followed by non-parametric bootstrapping with 5000 replicates to generate Felsenstein (FBP) branch support values for the best scoring tree, with convergence assessed post hoc using the autoMRE criterion.



Fig. 2 *Ulva fenestrata* specimens collected during this study. Clockwise from left: specimen SG-21-347 from South Georgia; specimens 021213-01iv, FLK503, FLK851 and FLK1058 from the Falkland Islands. Scalebars represent 5 cm. Specimen collection details are given in Online Resource 1

Results

Molecular phylogenetic analyses confirmed the presence of *U. fenestrata* in South Georgia (*tufA* and *rbc*L-3P; Fig. 3, Online Resources 4, 5) and the Falkland Islands (*tufA* only).

The *tufA* single-marker analysis produced two subclades within the *U. fenestrata* clade, one containing samples from the North Pacific, including the holotype from Kamchatka in Eastern Russia, and the other containing samples from South Georgia, the Falkland Islands and the North Atlantic, although these subclades were not well supported (Fig. 3). While *tufA* sequences were identical within each subclade, they differed by a single base pair (0.0015%) between subclades. For *rbc*L-3P, South Georgia *U. fenestrata* was resolved within a well-supported clade including the holotype and samples from Japan, New Zealand and both sides of the North Atlantic (Online Resource 4). While the South Georgia specimen was identical to the holotype in terms of *rbc*L-3P sequence, the maximum pairwise difference within the clade was 2 bp (0.0032%). The concatenated *tufA* + *rbc*L-3P analysis supported the single-marker results and did not provide any further resolution (Online Resource 5). While *U. fenestrata* appears to be widespread in the Falkland Islands, distributed from the southwest coast of West Falkland to the east coast of East Falkland (Fig. 1), the species was only collected from Grytviken Jetty in King Edward Cove on the north coast of South Georgia (Online Resource 1).

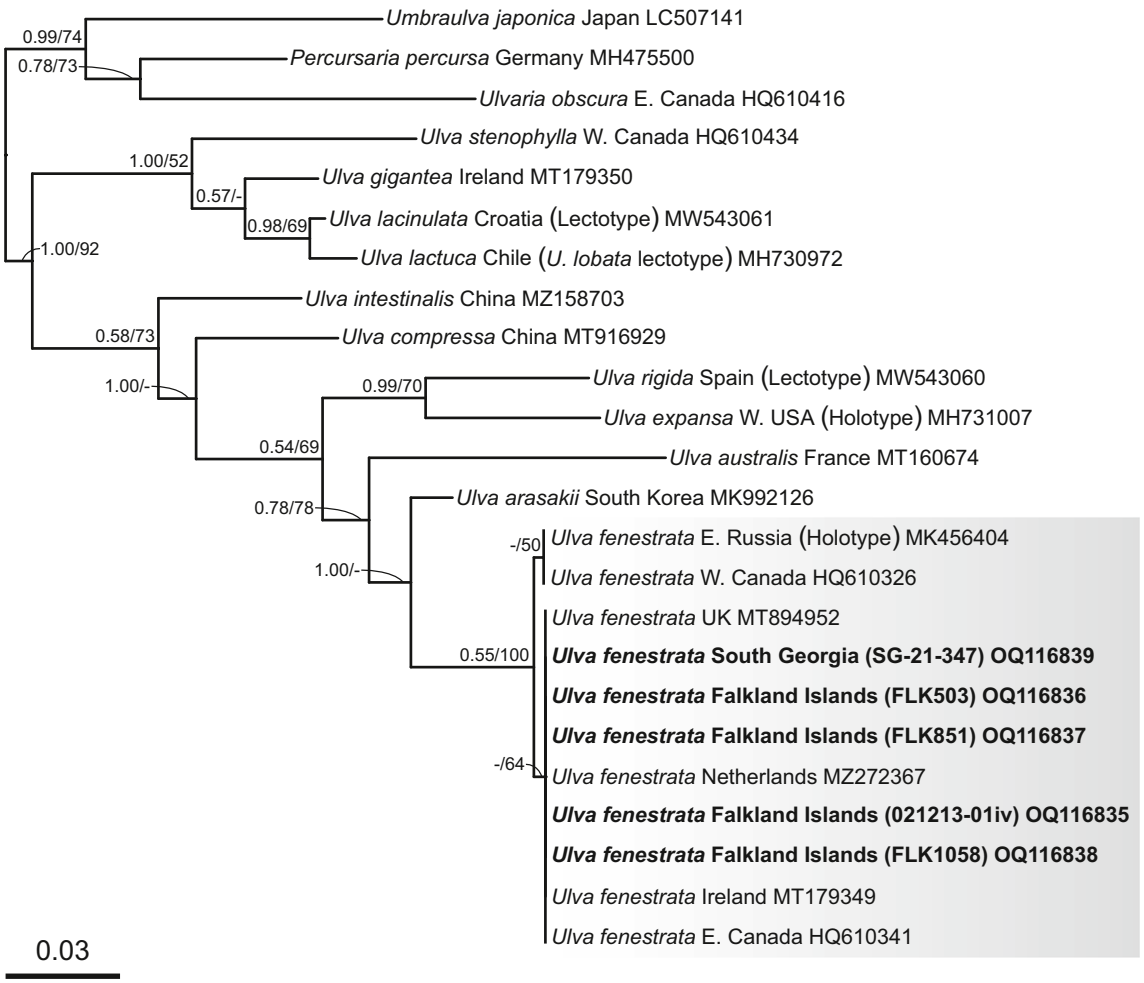


Fig. 3 Bayesian phylogenetic tree inferred for *tufA* sequence data. Node values indicate maximum likelihood bootstrap support values/Bayesian posterior probabilities ('–' denotes < 50% support). Clades with low overall support are collapsed for easier interpretation. The *Ulva fenestrata* clade is highlighted in grey, with samples from South Georgia and the Falkland Islands emphasised in bold. Scalebar represents number of substitutions per site

Discussion

This study provides the first evidence of a non-native seaweed, *U. fenestrata*, in South Georgia and confirms its establishment in the Falkland Islands, where it is now distributed widely. There is only one previous record of a non-native marine species in South Georgia, the mussel *Mytilus edulis*, a live individual of which was found at King Edward Point in 1974 (Ralph et al. 1976). Although this species appears not to have become established, it is still considered a high-risk potential invader (Dawson et al. 2022).

The genus *Ulva* is a good example with which to illustrate the problems in establishing whether a species is non-native and how long it has been in a particular area. High phenotypic variability combined with a lack of distinctive morphological characters means that molecular data are necessary to confirm species identities (Maggs et al. 2007; Saunders and Kucera 2010; Tran et al. 2022). As a result, the misapplication of species names is widespread within *Ulva*, and this has led to a misunderstanding of species distributions. *Ulva fenestrata* is a case in point. For about 250 years, the name *U. lactuca* was generally used for cold temperate *Ulva* species until Hughey et al. (2019) sequenced the holotype of *U. lactuca*, demonstrating that it was almost identical to the epitype of *U. fasciata* Delile, a species found in warm temperate to tropical seas. Having considered that the *U. lactuca* holotype was from the Indo-Pacific, the authors applied the earlier name *U. fenestrata* to the cold temperate Northern Hemisphere species (Hughey et al. 2019). Establishing the species concept of *U. fenestrata* demonstrates the importance of reliable taxonomy based on robust scientific and historical evidence for compiling accurate species lists and distinguishing taxa.

The length of time *U. fenestrata* has been present in South Georgia and the Falkland Islands is unknown. Based on the collecting date of specimen 021213-01iv in the current study, the species has been in the Falkland Islands since at least 2013. Other historical specimens in the Natural History Museum (BM) algal herbarium may represent this species based on morphological examination but require molecular confirmation. This includes 14 specimens identified as *U. lactuca* collected between 1842 and 2003 from a range of localities in West and East Falkland, raising the possibility that *U. fenestrata* has been present in the Falkland Islands for a long time. In the case of South Georgia, for which even fewer historical data exist, there are two specimens identified as *U. latissima* collected from Cumberland Bay and King Edward Cove in 1913. In a list of South Georgia seaweed species compiled from published records and BM herbarium specimens (John et al. 1994), the only species of *Ulva* listed was *U. lactuca* Linnaeus var. *macrogyna* [sic] Reinsch with the caveat "Status of this species requires confirmation". *Ulva lactuca* var. *macrogonya* Reinsch, which presumably is what John et al. (1994) referred to, is not an *Ulva* species. Reinsch (1890), who based his description on material collected from South Georgia in 1883, described this species as comprising a single layer of cells, whereas *Ulva* species are composed of two cell layers (Maggs et al. 2007). More recently, Wells et al. (2011) collected *U.* "*lactuca*" from King Edward Cove in 2010, which is a more likely candidate for *U. fenestrata*, awaiting identification via molecular analysis. Another specimen named *U. lactuca* was collected from Husvik Harbour during the same expedition, but this has since been identified as a species belonging to the genus *Protomonostroma* (Mrowicki, unpublished).

Until now, the only records of *U. fenestrata* in the Southern Hemisphere were from the South Island of New Zealand, relating to specimens collected from three disparate localities in 2003 and 2004 (Heesch et al. 2007, 2009), which were initially identified as *U. lactuca* but later confirmed as *U. fenestrata* (Hughey et al. 2019), now recognised as an introduced species in this region (Nelson et al. 2021). All three specimens were collected from artificial structures in harbours (Heesch et al. 2007), indicating human-mediated dispersal between sites. In South Georgia, the only confirmed (i.e. this study) and potential records of *U. fenestrata* are from King Edward Cove, the main port of entry, where the main settlement of King Edward Point and former whaling station of Grytviken are located, and which is frequented by tourist, research and fishing vessels of international origin. Further, two recent expeditions have surveyed and collected seaweeds extensively along the coast of South Georgia (Wells et al. 2011; Mrowicki and Brodie, unpublished) and found no evidence of *U. fenestrata* outside of this locality. This suggests that *U. fenestrata* was introduced to South Georgia via shipping, despite not necessarily during recent years, given that the island was a centre for sealing and whaling activity from the late 18th to mid-twentieth centuries (Hoffman et al. 2011; Calderan et al. 2020). It is also possible that this species arrived by 'hitchhiking' on drifting anthropogenic debris (Barnes 2002) or on seaweed rafts (Avila et al. 2020), which are known to travel thousands of kilometres around the Southern Ocean and act as vectors for species dispersal between distant landmasses, including South Georgia and New Zealand (Fraser et al. 2022). Determining the timeframe and pathway of introduction of *U. fenestrata* in South Georgia requires further investigation involving additional field sampling of remote areas in the Southern Hemisphere and detailed molecular analyses of historical and recent herbarium specimens. In particular, population genetics and genomic data may be

used to track the geographical origin of *U. fenestrata* and even predict its invasion success (Estoup and Guillemaud 2010; Matheson and McGaughran 2022), which would shed more light on its population status in South Georgia and other regions of the Southern Hemisphere where it is considered a non-native (Nelson et al. 2021).

Ulva species tend to be successful invaders compared to other seaweed taxa owing to their opportunistic life history and rapid growth rate, and this genus is highlighted as a target for monitoring and management (Williams and Smith 2007). DNA-barcoding studies have been instrumental in detecting non-native *Ulva* species in many parts of the world (e.g. Heesch et al. 2009; Krupnik et al. 2018; Steinhagen et al. 2019; Wei et al. 2022), including regions such as China where their rapid spread is causing severe ecological and economic impacts (Xie et al. 2020). For South Georgia, a recent horizon scanning study (Dawson et al. 2022) listed five seaweed species (none of which were *Ulva* species) as potential invasive non-natives in South Georgia, of which two were identified as "high-risk". In addition to these other seaweeds, our findings provide a baseline for monitoring *U. fenestrata* in South Georgia and emphasise the need for strict biosecurity measures to minimise the risk of introducing non-native species into potentially fragile ecosystems. This study also paves the way for more detailed molecular analyses of herbarium specimens to establish the likely timeframe, source and mode of arrival of *U. fenestrata* in South Georgia, providing further evidence to guide biosecurity policy.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00300-023-03136-6.

Acknowledgements This work was funded by Darwin Plus grants DPLUS122 "*Biodiversity discovery and the future of South Georgia's seaweed habitats*" and DPLUS068 "*Building foundations to monitor and conserve Falklands marine forest habitats*" awarded to Juliet Brodie. We thank the Government of South Georgia and the South Sandwich Islands and the crew of the MV Pharos SG for their support. We are also grateful to the South Atlantic Environmental Research Institute (SAERI), Shallow Marine Surveys Group (SMSG), Tritonia Scientific Ltd and the members of "Operation *Himantothallus*". This paper benefitted from discussions with Prof. Peter Convey (British Antarctic Survey) and Dan Bayley (SAERI).

Author contributions RJM and JB conceived research, conducted fieldwork, interpreted results, and wrote the manuscript. RJM conducted molecular laboratory work and analysed data.

Data availability Sequence data generated during this study are available via GenBank (Accessions OQ116835–OQ116840).

Declarations

Competing interests The authors declare no competing interests.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

References

Avila C, Angulo-Preckler C, Martín-Martín RP, Figuerola B, Griffiths HJ, Waller CL (2020) Invasive marine species discovered on non-native kelp rafts in the warmest Antarctic island. Sci Rep 10:1639. https://doi.org/10.1038/s41598-020-58561-y

Bailey SA, Brown L, Campbell ML, Canning-Clode J, Carlton JT, Castro N, Chainho P, Chan FT, Creed JC, Curd A, Darling J, Fofonoff P, Galil BS, Hewitt CL, Inglis GJ, Keith I, Mandrak NE, Marchini A, McKenzie CH, Occhipinti-Ambrogi A, Ojaveer H, Pires-Teixeira LM, Robinson TB, Ruiz GM, Seaward K, Schwindt E, Son MO, Therriault TW, Zhan A (2020) Trends in the detection of aquatic non-indigenous species across global marine, estuarine and freshwater ecosystems: a 50-year perspective. Divers Distrib 26:1780–1797. https://doi.org/10.1111/ddi.13167

Barnes DKA (2002) Invasions by marine life on plastic debris. Nature 416:808–809. https://doi.org/10.1038/416808a

Barnes DKA, Linse K, Waller C, Morley S, Enderlein P, Fraser KPP, Brown M (2006) Shallow benthic fauna communities of South Georgia Island. Polar Biol 29:223–228. https://doi.org/10.1007/s00300-005-0042-0

Bax N, Williamson A, Aguero M, Gonzalez E, Geeves W (2002) Marine invasive alien species: a threat to global biodiversity. Mar Policy 27:313–323. https://doi.org/10.1016/S0308-597X(03)00041-1

Bennett S, Santana-Garcon J, Marbà N, Jorda G, Anton A, Apostolaki ET, Cebrian J, Geraldi NR, Krause-Jensen D, Lovelock CE, Martinetto P, Pandolfi JM, Duarte CM, Tittensor D (2021) Climate-driven impacts of exotic species on marine ecosystems. Glob Ecol Biogeogr 30:1043–1055. https://doi.org/10.1111/geb.13283

Brodie J, Melbourne L, Mrowicki RJ, Brickle P, Russell S, Scott S (2021) *Corallina* (Corallinales, Rhodophyta) from Tristan da Cunha and the Falkland Islands: implications for South Atlantic biogeography. Eur J Phycol 56:94–104. https://doi.org/10.1080/09670262.2020.1780635

Calderan SV, Black A, Branch TA, Collins MA, Kelly N, Leaper R, Lurcock S, Miller BS, Moore M, Olson PA, Širović A, Wood AG, Jackson JA (2020) South Georgia blue whales five decades after the end of whaling. Endang Species Res 43:359–373. https://doi.org/10.3354/esr01077

Castresana J (2000) Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. Mol Biol Evol 17:540–552. https://doi.org/10.1093/oxfordjournals.molbev.a026334

Clubbe C, Ainsworth M, Bárrios S, Bensusan K, Brodie J, Cannon P, Chapman T, Copeland AI, Corcoran M, Sanchez MD, David JC, Dines T, Gardiner LM, Hamilton MA, Heller T, Hollingsworth PM, Hutchinson N, Llewelyn T, Forrest LL, McGinn KJ, Miles S, O'Donnell K, Woodfield-Pascoe N, Rich TCG, Rumsey F, Sim J, Smith SR, Spence N, Stanworth A, Stroh P, Taylor I,

Trivedi C, Twyford AD, Viruel J, Walker K, Wilbraham J, Woodman J, Fay MF (2020) Current knowledge, status and future for plant and fungal diversity in Great Britain and the UK Overseas Territories. Plants People Planet 2:557–579. https://doi.org/10.1002/ppp3.10142

Costello MJ, Dekeyzer S, Galil BS, Hutchings P, Katsanevakis S, Pagad S, Robinson TB, Turon X, Vandepitte L, Vanhoorne B, Verfaille K, Willan RC, Rius M (2021) Introducing the World Register of Introduced Marine Species (WRiMS). Manag Biol Invasions 12:792–811. https://doi.org/10.3391/mbi.2021.12.4.02

Dawson W, Peyton JM, Pescott OL, Adriaens T, Cottier-Cook EJ, Frohlich DS, Key G, Malumphy C, Martinou AF, Minchin D, Moore N, Rabitsch W, Rorke SL, Tricarico E, Turvey KMA et al (2022) Horizon scanning for potential invasive non-native species across the United Kingdom Overseas Territories. Conserv Lett. https://doi.org/10.1111/conl.12928

Estoup A, Guillemaud T (2010) Reconstructing routes of invasion using genetic data: why, how and so what? Mol Ecol 19:4113–4130. https://doi.org/10.1111/j.1365-294X.2010.04773.x

Famà P, Wysor B, Kooistra WHCF, Zuccarello GC (2002) Molecular phylogeny of the genus *Caulerpa* (Caulerpales, Chlorophyta) inferred from chloroplast *tufA* gene. J Phycol 38:1040–1050. https://doi.org/10.1046/j.1529-8817.2002.t01-1-01237.x

Fraser CI, Dutoit L, Morrison AK, Pardo LM, Smith SDA, Pearman WS, Parvizi E, Waters J, Macaya EC (2022) Southern Hemisphere coasts are biologically connected by frequent, long-distance rafting events. Curr Biol 32:3154–3160. https://doi.org/10.1016/j.cub.2022.05.035

Heesch S, Broom J, Neill K, Farr T, Dalen J, Nelson W (2007) Genetic diversity and possible origins of New Zealand populations of *Ulva*. Biosecurity New Zealand Technical Paper No: 2007/01. Ministry of Agriculture and Forestry, Wellington, New Zealand

Heesch S, Broom JES, Neill KF, Farr TJ, Dalen JL, Nelson WA (2009) *Ulva*, *Umbraulva* and *Gemina*: genetic survey of New Zealand taxa reveals diversity and introduced species. Eur J Phycol 44:143–154. https://doi.org/10.1080/09670260802422477

Hoffman JI, Grant SM, Forcada J, Phillips CD (2011) Bayesian inference of a historical bottleneck in a heavily exploited marine mammal. Mol Ecol 20:3989–4008. https://doi.org/10.1111/j.1365-294X.2011.05248.x

Hogg OT, Barnes DKA, Griffiths HJ (2011) Highly diverse, poorly studied and uniquely threatened by climate change: an assessment of marine biodiversity on South Georgia's continental shelf. PLoS ONE 6:e19795. https://doi.org/10.1371/journal.pone.0019795

Hughey JR, Maggs CA, Mineur F, Jarvis C, Miller KA, Shabaka SH, Gabrielson PW (2019) Genetic analysis of the Linnaean *Ulva lactuca* (Ulvales, Chlorophyta) holotype and related type specimens reveals name misapplications, unexpected origins, and new synonymies. J Phycol 55:503–508. https://doi.org/10.1111/jpy.12860

John DM, Pugh PJA, Tittley I (1994) Observations on the benthic marine algal flora of South Georgia: a floristic and ecological analysis. Bull Nat Hist Mus 24:101–114

Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usability. Mol Biol Evol 30:772–780. https://doi.org/10.1093/molbev/mst010

Kozlov AM, Darriba D, Flouri T, Morel B, Stamatakis A (2019) RAxML-NG: a fast, scalable and user-friendly tool for maximum likelihood phylogenetic inference. Bioinformatics 35:4453–4455. https://doi.org/10.1093/bioinformatics/btz305

Krupnik N, Paz G, Douek J, Lewinsohn E, Israel A, Carmel N, Mineur F, Maggs CA (2018) Native, invasive and cryptogenic *Ulva* species from the Israeli Mediterranean Sea: risk and potential. Mediterr Mar Sci 191:132–146. https://doi.org/10.12681/mms.2104

Lanfear R, Frandsen PB, Wright AM, Senfeld T, Calcott B (2016) PartitionFinder 2: new methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. Mol Biol Evol 34:772–773. https://doi.org/10.1093/molbev/msw260

Maggs CA, Blomster J, Mineur F, Kelly J (2007) Ulva. In: Brodie J, Maggs CA, John DM (eds) Green seaweeds of Britain and Ireland. Dataplus Print & Design, Northern Ireland, pp 80–103

Manhart JR (1994) Phylogenetic analysis of green plant *rbc*L sequences. Mol Phylogenet Evol 3:114–127. https://doi.org/10.1006/mpev.1994.1014

Matheson P, McGaughran A (2022) Genomic data is missing for many highly invasive species, restricting our preparedness for escalating incursion rates. Sci Rep 12:13987. https://doi.org/10.1038/s41598-022-17937-y

Nelson WA, D'Archino R, Neill KF, Robinson NM (2021) Introduced marine macroalgae: new perspectives on species recognition and distribution in New Zealand. Bot Mar 64:379–393. https://doi.org/10.1515/bot-2021-0042

Okonechnikov K, Golosova O, Fursov M, UGENE team (2012) Unipro UGENE: a unified bioinformatics toolkit. Bioinformatics 28:1166–1167. https://doi.org/10.1093/bioinformatics/bts091

Ralph R, Maxwell JGH, Everson I, Hall J (1976) A record of *Mytilus edulis* L. from South Georgia. Br Antarct Surv Bull 44:101–102

Rambaut A, Drummond AJ, Xie D, Baele G, Suchard MA (2018) Posterior summarization in Bayesian phylogenetics using Tracer 1.7. Syst Biol 67:901–904. https://doi.org/10.1093/sysbio/syy032

Reinsch PF (1890) Zur Meeresalgen flora von Süd-Georgien. In: von Neumayer G (ed) Die internationale Polarforschung 1812–1883: Geschichlicher Theil und in einem Anhange mehrer einzlene Abhanlungen physikalischen und sonstigen Inhalts. Band. II Bescheibende Naturwissenschaften. Verlag von A, Asher, pp 366–449

Rogers AD, Yesson C, Gravestock P (2015) A biophysical and economic profile of South Georgia and the South Sandwich Islands as potential large-scale Antarctic protected areas. In: Curry BE (ed) Advances in marine biology, vol 70. Academic Press, Oxford, pp 1–286

Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Syst Biol 61:539–542. https://doi.org/10.1093/sysbio/sys029

Saunders GW, Kucera H (2010) An evaluation of *rbc*L, *tufA*, UPA, LSU and ITS as DNA barcode markers for the marine green macroalgae. Cryptogam Algol 31:487–528

Steinhagen S, Karez R, Weinberger F (2019) Cryptic, alien and lost species: molecular diversity of Ulva sensu lato along the German coasts of the North and Baltic Seas. Eur J Phycol 54:466–483. https://doi.org/10.1080/09670262.2019.1597925

Thomsen MS, Wernberg T, South PM, Schiel DR (2016a) Non-native seaweeds drive changes in marine coastal communities around the world. In: Hu ZM, Fraser C (eds) Seaweed phylogeography. Springer, Dordrecht, pp 147–185

Thomsen MS, Wernberg T, Staehr PA, Schiel D (2016b) Ecological interactions between marine plants and alien species. In: Ólafsson E (ed) Marine macrophytes as foundation species. CRC Press, Boca Raton, pp 226–258

Tran LAT, Vieira C, Steinhagen S, Maggs CA, Hiraoka M, Shimada S, Van Nguyen T, De Clerck O, Leliaert F (2022) An appraisal

of *Ulva* (Ulvophyceae, Chlorophyta) taxonomy. J Appl Phycol 34:2689–2703. https://doi.org/10.1007/s10811-022-02815-x

Wei X, Liu W, Lin X (2022) First record of *Ulva californica* in the mainland of China: a single alien parthenogenetic population in discontinuous distribution. J Oceanol Limnol 40:2343–2353. https://doi.org/10.1007/s00343-022-1392-y

Wells E, Brewin P, Brickle P (2011) Intertidal and subtidal benthic seaweed diversity of South Georgia. Report for the South Georgia Heritage Trust—Survey September 2011. Shallow Marine Surveys Group, Stanley, Falkland Islands

Williams SL, Smith JE (2007) A global review of the distribution, taxonomy, and impacts of introduced species. Annu Rev Ecol Evol Syst 38:327–359. https://doi.org/10.1146/annurev.ecolsys.38.091206.095543

Xie WF, Wu CH, Zhao J, Lin XY, Jiang P (2020) New records of *Ulva* spp. (Ulvophyceae, Chlorophyta) in China, with special reference to an unusual morphology of *U. meridionalis* forming green tides. Eur J Phycol 55:412–425. https://doi.org/10.1080/09670262.2020.1740946

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.