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Ulva* L. (Ulvales, Chlorophyta) from Manawatāwhi/ Three Kings Islands, New Zealand: *Ulva piritoka* Ngāti Kuri, Heesch & W.A.Nelson, sp. nov. and records of two non-native species, *U. compressa* and *U. rigida

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ABSTRACT

Manawatāwhi/Three Kings Islands lie to the north of the North Island of New Zealand. Manawatāwhi is part of the rohe (territory) of Ngāti Kuri, with the islands having spiritual, cultural, political and customary significance. This group of small islands has one of the most pristine coastlines in New Zealand, with no human-mediated impacts from current land use, no permanent anchorage points, and landing on the islands is prohibited. The islands harbour a rich marine biota with a number of endemic species. A recent collection trip and molecular genetic studies using the *rbcL* marker revealed the presence of three entities of the genus *Ulva* L. (Ulvales, Chlorophyta) on the islands. One of these we describe herein as *Ulva piritoka* Ngāti Kuri, Heesch & W.A.Nelson, sp. nov. While it is genetically close to *U. adhaerens* Matsumoto & Shimada from Japan, differences in morphology, habitat and *rbcL* gene region, including the presence of a large group II intron in *U. adhaerens*, which was lacking in the Manawatāwhi specimen, led us to conclude *U. piritoka* sp. nov. belongs to a distinct species. We also confirmed the presence of *Ulva compressa* L. and *Ulva rigida* C.Agardh, both of which, although present on the New Zealand mainland, were originally described from Europe and are considered introductions to the New Zealand archipelago. These are the first reported marine non-indigenous species (NIS) recorded from Manawatāwhi/Three Kings Islands, and the implications of their presence are discussed.

KEY WORDS

Manawatāwhi,
New Zealand,
Ngāti Kuri,
rbcL,
Ulvales,
Three Kings Islands,
new species.

RÉSUMÉ

Ulva L. (Ulvales, Chlorophyta) des îles des Trois Rois, Nouvelle-Zélande: *Ulva piritoka* Ngāti Kuri, Heesch & W.A.Nelson, sp. nov. et signalement de deux espèces non indigènes, *U. compressa* et *U. rigida*.

Manawatāwhi/les îles des Trois Rois se trouvent au nord de l'île du Nord de la Nouvelle-Zélande. Manawatāwhi fait partie du rohe (territoire) de Ngāti Kuri, dont les îles ont une signification spirituelle, culturelle, politique et coutumière. Ce groupe de petites îles abritent l'un des littoral les plus vierge de la Nouvelle-Zélande, sans impact de l'homme lié à l'utilisation actuelle des terres, sans point d'ancrage permanent, et le débarquement sur les îles est interdit. Les îles abritent un riche biote marin avec de nombreuses espèces endémiques. Un récent voyage de collecte et des études de génétique moléculaire utilisant le marqueur *rbcL* ont révélé la présence de trois entités du genre *Ulva* L. (Ulvales, Chlorophyta) sur les îles. Parmi celles-ci, nous décrivons ici une nouvelle espèce *Ulva piritoka* Ngāti Kuri, Heesch & W.A.Nelson, sp. nov. Bien qu'elle soit génétiquement proche de *U. adhaerens* Matsumoto & Shimada du Japon, les différences dans la morphologie, l'habitat et la région du gène *rbcL*, y compris la présence d'un grand intron de groupe II dans *U. adhaerens* qui manquait dans le spécimen de Manakatāwhi, nous a amenés à conclure *U. piritoka* sp. nov. appartient à une espèce distincte. Nous avons également confirmé la présence d'*Ulva compressa* L. et d'*Ulva rigida* C.Agardh, qui, bien que présents sur le continent néo-zélandais, ont été décrits à l'origine d'Europe et sont considérés comme des introductions dans l'archipel néo-zélandais. Il s'agit des premières espèces non indigènes (NIS) marines signalées à Manawatāwhi/les îles des Trois Rois, et les implications de leur présence sont discutées.

MOTS CLÉS
Manawatāwhi,
Ngāti Kuri,
Nouvelle-Zélande,
rbcL,
Ulvales,
îles des Trois Rois,
espèce nouvelle.

INTRODUCTION

Ulva L. (Ulvales, Chlorophyta) is a large, globally distributed genus, with 131 species currently accepted taxonomically (Guiry & Guiry 2021). Species of *Ulva* are found in a wide range of habitats and are notoriously difficult to identify using morphological and anatomical features alone as they exhibit considerable phenotypic plasticity (e.g. Steinhagen *et al.* 2019). They are among the most common fouling organisms on vessel hulls and are ideal candidates for human-mediated dispersal with numerous species able to tolerate a broad range of physical conditions (Schaffelke *et al.* 2006).

The correct application of names within the genus *Ulva* remains a major issue. Recent genetic analysis of the genericity of *Ulva*, *Ulva lactuca* L., as well as type material of a number of other species, is a major step forward in resolving these issues (e.g. Hughey *et al.* 2019), as are regional genetic surveys to better understand the biodiversity of the genus (e.g. Shimada *et al.* 2003; Kraft *et al.* 2010; O'Kelly *et al.* 2010; Kirkendale *et al.* 2013; Krupnik *et al.* 2018). Heesch *et al.* (2007, 2009) conducted a genetic survey of the genus *Ulva* species in New Zealand, covering many stretches of the accessible coast line, as well as both intertidal and subtidal habitats, to determine the entities present in the region. Based on that study, there are currently 17 species of *Ulva* recognised in the New Zealand flora, of which eight are regarded as non-native based on their global and local distributions (Neill & Nelson 2019).

Recent macroalgal collections from Manawatāwhi / Three Kings Islands, New Zealand (by an expedition led by Auckland Museum Tāmaki Paenga Hira including WAN) included specimens of *Ulva*, enabling the first genetic analyses for material from this part of the New Zealand archipelago. This isolated cluster of thirteen uninhabited islands, just 6.85 km² in area,

lies 55 km to the north of Te Rerenga Wairua/ Cape Reinga of the North Island of New Zealand (Fig. 1). The coastline of Manawatāwhi is one of most pristine in the New Zealand region: there are no human-mediated impacts from current land use, no commercial fisheries harvest of coastal herbivores, no jetties or permanent anchorage points, and landing on the islands (classified as a nature reserve) is prohibited.

The macroalgal flora of the islands contains a number of endemic genera (e.g. *Perisporochmus* V.J.Chapm., *Chlidophyllum* W.A.Nelson, *Perplexiramosus* W.A.Nelson & D'Archino) as well as endemic species (e.g. *Adamsiella melchior* L.E.Phillips & W.A.Nelson, *Curdiea balthazar* W.A.Nelson, G.A.Knight & R.Falshaw, *Dictyota korowai* W.A.Nelson, J.E.Sutherland & Ngāti Kuri, *Landsburgia ilicifolia* W.A.Nelson, *Polycoelia kurariirapa* D'Archino, Zuccarello & Ngāti Kuri, *Sargassum johnsonii* V.J.Chapm.) (Chapman 1954, 1961; Nelson 1999b; Nelson *et al.* 1999; Phillips 2002; Nelson & D'Archino 2014; D'Archino *et al.* 2020).

Manawatāwhi is part of the rohe (territory) of Ngāti Kuri, with the islands having spiritual, cultural, political and customary significance. As kaitiaki (guardians/stewards), Ngāti Kuri seek to understand and protect the biota dwelling on land and in the seas around these islands, regarding the biota as taonga (treasures) and recognising the national and international significance of the unique diversity and assemblages found at Manawatāwhi. One of the current priorities for Ngāti Kuri is not only the documentation of the species occurring within their rohe but also their capacity to engage and contribute to knowledge making. The research reported here is part of an on-going research collaboration on the rimurimu (macroalgae) of these islands and the naming of this unique flora (*Dictyota korowai* – Nelson *et al.* 2019; *Polycoelia kurariirapa* – D'Archino *et al.* 2020).



FIG. 1. — Map of northern New Zealand showing the position of Manawatāwhi/Three Kings Islands.

In this paper we describe a new species of native *Ulva* and report the presence at Manawatāwhi of two other species we consider introductions to the New Zealand archipelago.

MATERIAL AND METHODS

MATERIAL

Specimens were collected during the Manawatāwhi / Three Kings Expedition in 2013 led by Tāmaki Paenga Hira Auckland Museum and are deposited in the herbarium of Tāmaki Paenga Hira Auckland Museum (AK: herbarium abbreviation,

Thiers 2020). Subsamples for phylogenetic analyses were dried in silica gel, and in some cases, further subsamples were also preserved in 5% formalin for morphological observations. One collection of *Ulva* was made intertidally and four other collections subtidally at depths of 14–24 m.

MORPHOLOGICAL OBSERVATIONS

Overall gross morphologies of collected specimens were evaluated macroscopically, to distinguish specimens of *Ulva* from those belonging to the related genus *Umbraulva*. Anatomical observations were made from hand sections of thalli which were either mounted unstained in 50% Karo light corn syrup

TABLE 1. — Collection details and accession numbers for *Ulva* specimens from Manawatāwhi/Three Kings Islands. Herbarium abbreviations according to Thiers (continuously updated) (–, no data; n/a, not applicable).

Species	Sample label	Collection information: site; collector, date	Herbarium accession no.	ENA/GenBank accession no. for <i>rbcL</i>
<i>Ulva compressa</i> L.	ASN621	Tasman Bay, Manawatāwhi, 34°9'18.6"S, 172°8'59.4"E, high intertidal; TK2013-57, R. D'Archino, 17.IV.2013	AK379913	MW389663
<i>Ulva piritoka</i> Ngāti Kuri, Heesch & W.A.Nelson, sp. nov.	ASN740	Tasman Bay, Manawatāwhi, 34°9'13"S, 172°8'41.5"E; subtidal: 15 m depth; R. D'Archino, 19.IV.2013	AK379911	MW389665
<i>Ulva rigida</i> C.Agardh	ASN596	Tasman Bay, Manawatāwhi, 34°9'9"S, 172°8'58.2"E; subtidal: 22-24 m depth; TK2013-57, R. D'Archino, 17.IV.2013	AK379912	MW389664

TABLE 2. — Published *rbcL* sequences used in the phylogenetic analyses. Current nomenclature according to Guiry & Guiry (2021).

Species	Country of origin; Reference	ENA/GenBank accession no.
<i>Gemina letterstedtioidea</i> V.J.Chapman	New Zealand; Heesch <i>et al.</i> (2009)	EF110068
<i>Percursaria percurta</i> (C.Agardh) Rosenvinge	UWCC MA230; Hayden <i>et al.</i> (2003)	AF499674
<i>Ryugophycus kuaweuweu</i> (H.L.Spalding & A.R.Sherwood) H.Kawai, T.Hanyuda & T.Kitayama	New Zealand; Heesch <i>et al.</i> (2009) (as <i>Umbraulva</i> 'Kermadecs.')	EF110288
<i>Ulva aragoensis</i> (Bliding) Maggs	Hawaii; Spalding <i>et al.</i> (2016)	KT932987
<i>Ulva arasakii</i> M.Chihara	Israel; Krupnik <i>et al.</i> (2018)	MG704815
<i>Ulva australis</i> Areschoug	Japan; Shimada <i>et al.</i> (2003)	AB097621
<i>Ulva brisbanensis</i> L.G.Kraft, Kraft & R.F.Waller	Japan; Hayden & Waaland (2004)	AY422549
	New Zealand; Heesch <i>et al.</i> (2009) (as <i>U. pertusa</i> Kjellman)	EF109975
	Australia; Kraft <i>et al.</i> (2010)	EU933945
<i>Ulva californica</i> Wille	United States; Hayden <i>et al.</i> (2003)	AY255866
<i>Ulva chaugulii</i> M.G.Kavale & M.A.Kazi	New Zealand; Heesch <i>et al.</i> (2009)	EF110039
	Israel; Krupnik <i>et al.</i> (2018)	MG704805
<i>Ulva clathrata</i> (Roth) C.Agardh	Spain; Hayden & Waaland (2004)	AY422563
<i>Ulva cf. clathratioides</i>	New Zealand; Heesch <i>et al.</i> (2009) (as <i>Ulva</i> sp. 2)	EF110022
<i>Ulva clathratioides</i> L.G.Kraft, Kraft & R.F.Waller	Australia; Kraft <i>et al.</i> (2010)	EU933940
<i>Ulva compressa</i> L.	New Zealand; Heesch <i>et al.</i> (2009)	EF110272
<i>Ulva fenestrata</i> Postels & Ruprecht	Ireland; Loughnane <i>et al.</i> (2008)	EU484397
	New Zealand; Heesch <i>et al.</i> (2009) (as <i>Ulva lactuca</i> L.)	EF110114
<i>Ulva gigantea</i> (Kützinger) Bliding	Ireland; Loughnane <i>et al.</i> (2008)	EU484398
	Ireland; Loughnane <i>et al.</i> (2008)	EU484403
<i>Ulva howensis</i> (A.H.S.Lucas) Kraft	Canada; Saunders & Kucera (2010)	HQ603535
	Australia; Kraft <i>et al.</i> (2010)	EU933948
<i>Ulva iliohaha</i> H.L.Spalding & A.R.Sherwood	Australia; Kirkendale <i>et al.</i> (2013)	JN082214
	Japan; Ichihara <i>et al.</i> (2013)	AB741536
<i>Ulva intestinalis</i> L.	Hawaii; Kawai <i>et al.</i> (2020)	LC507130
	United Kingdom; Hayden <i>et al.</i> (2003)	AY255860
	New Zealand; Heesch <i>et al.</i> (2009)	EF110276
<i>Ulva lactuca</i> L.	Norway; Biancarosa <i>et al.</i> (2016)	LN877859
	Hawaii; Hayden & Waaland (2004) (as <i>Ulva fasciata</i> Delile)	AY422565
<i>Ulva lobata</i> (Kützinger) Harvey	New Zealand; Heesch <i>et al.</i> (2009) (as <i>Ulva fasciata</i>)	EF110500
	United States; Hayden <i>et al.</i> (2003)	AY255868
<i>Ulva ohnoi</i> M.Hiraoka & S.Shimada	Canada; Saunders & Kucera (2010)	HQ603604
<i>Ulva partita</i> K.Ichihara	Japan; Hiraoka <i>et al.</i> (2004)	AB116040
<i>Ulva procera</i> (K.Ahlner) H.S.Hayden, Blomster, Maggs, P.C.Silva, Stanhope & Waaland	Japan; Ichihara <i>et al.</i> (2015)	LC021415
	Japan; Hayden & Waaland (2004)	AY422562
<i>Ulva prolifera</i> O.F.Müller	New Zealand; Heesch <i>et al.</i> (2009)	EF110255
	United Kingdom; Hayden <i>et al.</i> (2003)	AY255864
<i>Ulva pseudorotundata</i> Cormaci, G.Furnari & Alongi	New Zealand; Heesch <i>et al.</i> (2009)	EF110236
	Ireland; Loughnane <i>et al.</i> (2008)	EU484401
<i>Ulva reticulata</i> Forskål	Ireland; Wan <i>et al.</i> (2017)	HG940508
<i>Ulva rigida</i> C.Agardh	Philippines; Shimada <i>et al.</i> (2003)	AB097635
	United Kingdom; Hayden <i>et al.</i> (2003) (as <i>Ulva scandinavica</i> Bliding)	AY255870
	New Zealand; Heesch <i>et al.</i> (2009) (as <i>Ulva</i> sp.)	EF110044
<i>Ulva simplex</i> (K.L.Vinogradova) H.S.Hayden, Blomster, Maggs, P.C.Silva, Stanhope & Waaland	Ireland; Loughnane <i>et al.</i> (2008)	EU484395
	South Korea; Kang <i>et al.</i> (2014)	KP233772
	Japan; Ogawa <i>et al.</i> (2013)	AB830517

TABLE 2. — continuation.

<i>Ulva</i> sp.	Japan; Ogawa <i>et al.</i> (2013) Australia; Kraft <i>et al.</i> (2010) Hawaii; O’Kelly <i>et al.</i> (2010)	AB830527 EU933963 GU138287, GU138252
	USA; Guidone <i>et al.</i> (2013)	KC582349
<i>Ulva</i> sp. 4	New Zealand; Heesch <i>et al.</i> (2009)	EF109945
<i>Ulva</i> sp. 5	New Zealand; Heesch <i>et al.</i> (2009)	EF110204
<i>Ulva</i> sp. 6	New Zealand; Heesch <i>et al.</i> (2009)	EF110460
<i>Ulva</i> sp. 9	New Zealand; Heesch <i>et al.</i> (2009)	EF110466
<i>Ulva</i> sp. 10	New Zealand; Heesch <i>et al.</i> (2009)	EF110444
<i>Ulva spinulosa</i> Okamura & Segawa	Japan; Shimada <i>et al.</i> (2003)	AB097636
<i>Ulva stenophylla</i> Setchell & N.L.Gardner	United States; Hayden <i>et al.</i> (2003)	AY255874
<i>Ulva cf stenophylloides</i>	Chile; Hayden <i>et al.</i> (2003) (as <i>Ulva</i> sp. 1) New Zealand; Heesch <i>et al.</i> (2009) (as <i>Ulva</i> sp. 1)	AY255871 EF109979
<i>Ulva stenophylloides</i> L.G.Kraft, Kraft & R.F.Waller	Australia; Kraft <i>et al.</i> (2010)	EU933950
<i>Ulva taeniata</i> (Setchell) Setchell & N.L.Gardner	United States; Hayden & Waaland (2004)	AY422567
<i>Ulva tanneri</i> H.S.Hayden & Waaland	Japan; Hayden <i>et al.</i> (2003)	AY255858
<i>Ulvaria splendens</i> (Ruprecht) K.L.Vinogradova	Japan; Shimada <i>et al.</i> (2003)	AB097611
<i>Umbraulva amamiensis</i> (Tanaka) Bae & I.K.Lee	Japan; Shimada <i>et al.</i> (2003)	AB097614
<i>Umbraulva japonica</i> (Holmes) Bae & I.K.Lee	Japan; Shimada <i>et al.</i> (2003)	AB097613
<i>Umbraulva kaloakulau</i> H.L.Spalding & A.R.Sherwood	Hawaii; Spalding <i>et al.</i> (2016)	KT932990
<i>Umbraulva dangeardii</i> M.J.Wynne & G.Furnari	New Zealand; Heesch <i>et al.</i> (2009) (as <i>Umbraulva olivascens</i> (P.J.L.Dang.) Bae & I.K.Lee) Ireland; Loughnane <i>et al.</i> (2008)	EF110112 EU484405

or stained prior to mounting with 1% aqueous aniline blue acidified with 1% hydrochloric acid. Photomicrographs were taken using an Olympus BX53 (Tokyo, Japan) with a SC100 (Olympus, Münster, Germany) digital camera.

MOLECULAR SYSTEMATICS

Whole genomic DNA was extracted from *c.* 10 mg silica gel-dried plant tissue subsamples with the NucleoSpin® Plant II kit [Macherey-Nagel, Düren, Germany], following the instructions of the manufacturer. Polymerase chain reactions (PCR) used published primers (SH F1 and SH R4, Heesch *et al.* 2009) to amplify the plastid-encoded *rbcL* gene marker (encoding the large subunit of the Ribulose Biphosphate Carboxylase-Oxygenase, RuBisCO). PCR amplification, product clean-up, and sequencing followed methods described in Heesch *et al.* (2016).

Sequence quality was assessed by eye in 4Peaks v.1.7.2 (Griekspoor & Groothuis 2005). Sequences were aligned manually in PhyDE version 0.9971 (Müller *et al.* 2010), together with published sequences. Related species of Ulvaceae served as outgroups for phylogenetic analyses, i.e. *Percursaria percura* (C.Agardh) Rosenvinge, various species of the genus *Umbraulva* E.H.Bae & I.K. Lee, *Ulvaria splendens* (Ruprecht) K.L.Vinogradova, and *Gemina letterstedtioidea* V.J.Chapm. (for GenBank/ENA accession numbers and respective references see Table 2).

An alignment containing 76 sequences over a length of 1250 bases was transferred to formats suitable for subsequent phylogenetic analyses using the online tool ALTER (ALIGNment Transformative EnviRonment; Glez-Peña *et al.* 2010). Phylogenetic analyses followed methods given in Heesch *et al.*

(2009), with maximum likelihood (ML) optimality criteria analysed in RaxML v.7.2.2 (Stamatakis 2006) using the default GTR model of evolution, and Bayesian posterior probabilities generated in MrBayes v. 3.2.6 x64 (Huelsenbeck & Ronquist 2001; Ronquist *et al.* 2012).

RESULTS

FIELD OBSERVATIONS

Specimens from three subtidal collections possessed a very distinctive morphology and were recorded as “*Ulva*- prostrate” in field notes. They were found to be growing closely against rock surfaces, with an unattached, undulating margin. Although the thalli were quite small (*c.* 1–2 cm in diameter), they were found growing in quite extensive patches (Fig. 2).

The intertidal collection consisted of specimens that were small in stature (up to 4 cm in height) consisting of narrow tubular thalli (AK379913; 17.IV.2013; TK2013-57; 34°9’18.6”S, 172°8’59.4”E). One subtidal collection consisted of four small upright blades (maximum height 1 cm) (AK379912; 14-19 m; 17.IV.13; 34°9’9”S, 172°8’58.2”E).

MOLECULAR ANALYSES

New partial *rbcL* sequences were obtained from three samples collected in this study, representing three distinct genetic entities. The sample of prostrate *Ulva*, when compared with available sequence data in GenBank, was found to be most closely related to the Japanese species *Ulva adhaerens* Matsu-moto & Shimada, differing by five substitutions in the exon (over 1149 base pairs) and by the presence in *U. adhaerens*



FIG. 2. — Subtidal patches of *Ulva piritoka* Ngāti Kuri, Heesch & W.A.Nelson, sp. nov.

of a Group II intron (Matsumoto & Shimada 2015). We describe this entity as a new species of *Ulva*.

When compared to published sequence data available in GenBank, the sequence data from our collected intertidal sample of *Ulva* (herbarium accession AK379913) corresponded to accessions of *Ulva compressa* L., and sequence data from the small bladed *Ulva* (herbarium accession AK379912) corresponded to accessions of *Ulva rigida* C.Agardh (Fig. 3).

Ulva piritoka

Ngāti Kuri, Heesch & W.A.Nelson, sp. nov.
(Figs 2; 4-6)

HOLOTYPE. — AK379911, R.D'Archino, 19.IV.2013, 15 m depth (Fig. 4)

TYPE LOCALITY. — Tasman Bay, Manawatāwhi, New Zealand (34°9'13"S, 172°8'41.5"E).

DIAGNOSIS. — Thalli prostrate, 1-2 cm in diameter, attached to substrate by scattered clumps of rhizoids on the lower blade surface, margins unattached with a ruffled /undulating appearance (Fig. 2). Thallus distromatic, cells rectangular; 45-55 µm thick at edge; becoming thicker in central regions (90-165 µm) with adaxial cell layer becoming deeper (80-100 µm) than the abaxial cell layer (40-60 µm). Rhizoids develop from both of the cell layers and join to form rhizoidal clumps 50-140 µm in diameter extending from the lower thallus surface to 180-220 µm in length (Figs 5A, B).

HABITAT. — Subtidal on rock and non-geniculate coralline algae, growing in patches on boulders, rocky reef and also found on stable cobbles and stones.

ETYMOLOGY. — *piri* (to stick, adhere, cling, keep close), *toka* (rock); in reference to the habit of this species, clinging tightly to the surface of rocks and withstanding the constant flow of current.

REPRESENTATIVE MATERIAL. — AK379910, R.D'Archino, 17.IV.13, TK2013-54, 14-19 m, 34°9'9"S, 172°8'58.2"E; ASN591, R.D'Archino, 17.IV.13, TK2013-51, 23-25 m, 34°9'14.8"S, 172°8'51.1"E.

COMMENTS

Underwater images from the islands show *Ulva piritoka* Ngāti Kuri, Heesch & W.A.Nelson, sp. nov. to occur commonly on a range of rocky substrata, sometimes forming extensive patches. It was seen to grow on bare rock as well as over non-geniculate corallines and also interspersed with sponge and other encrusting benthic species.

DISCUSSION

The islands of Manawatāwhi and the surrounding shelf region are known to be home to a very rich marine biota with many endemic species reported across all phyla (Arnold 2004). The discovery of new macroalgal taxa in this region is not surprising as the area remains poorly explored, in part because of its remoteness, and as a consequence of the challenges of working in an area that is very exposed to oceanic conditions with no sheltered shores.

Although the *rbcL* exon sequence of *Ulva piritoka* Ngāti Kuri, Heesch & W.A.Nelson, sp. nov. is similar to that of *U. adhaerens*, we consider there are sufficient differences to warrant recognition of *U. piritoka* sp. nov. as a distinct species: there are some clades of *Ulva* that have comparable differences in *rbcL* between currently valid species, e.g. *U. californica* vs *U. aragoensis* (4-7 bp); *U. ohnoi* vs *U. reticulata* (2 bp) and *U. ohnoi* vs *U. spinolosa* & *U. taeniata* (4 bp) (Hayden *et al.* 2003; Shimada *et al.* 2003; Hayden & Waaland 2004; Hiraoka *et al.* 2004; Heesch *et al.* 2009; Krupnik *et al.* 2018). *Ulva piritoka* sp. nov. and *U. adhaerens* differ in their geographic distributions (the isolated islands of Manawatāwhi, New Zealand, compared with coastal Honshu in Sagami Bay at Tenjin-jima, Yokosuka, Japan), as well as in their ecological distribution/habitat (subtidal, 14-25 m depth, on exposed oceanic islands, versus an intertidal rocky shore habitat for *U. adhaerens*). Moreover, there are some, albeit slight, morphological differences. The blades of *Ulva piritoka* sp. nov. were thinner at the margins becoming deeper in the centre of the thalli (45-165 µm) when compared with *U. adhaerens* (50-110 µm). The interlayer space between the adaxial and abaxial cells became very expanded in *U. adhaerens*, but this was not seen in *U. piritoka* sp. nov. When described by Matsumoto & Shimada (2015), *U. adhaerens* was considered to be unique amongst *Ulva* in producing rhizoids in distromatic regions other than the base; however, the development of multiple rhizoidal attachment points on a single thallus is also found in its sister species *U. piritoka* sp. nov.

The *rbcL* gene of *Ulva adhaerens* contains a Group II intron while that of *U. piritoka* Ngāti Kuri, Heesch & W.A.Nelson, sp. nov. does not. Group II introns are mobile elements that can

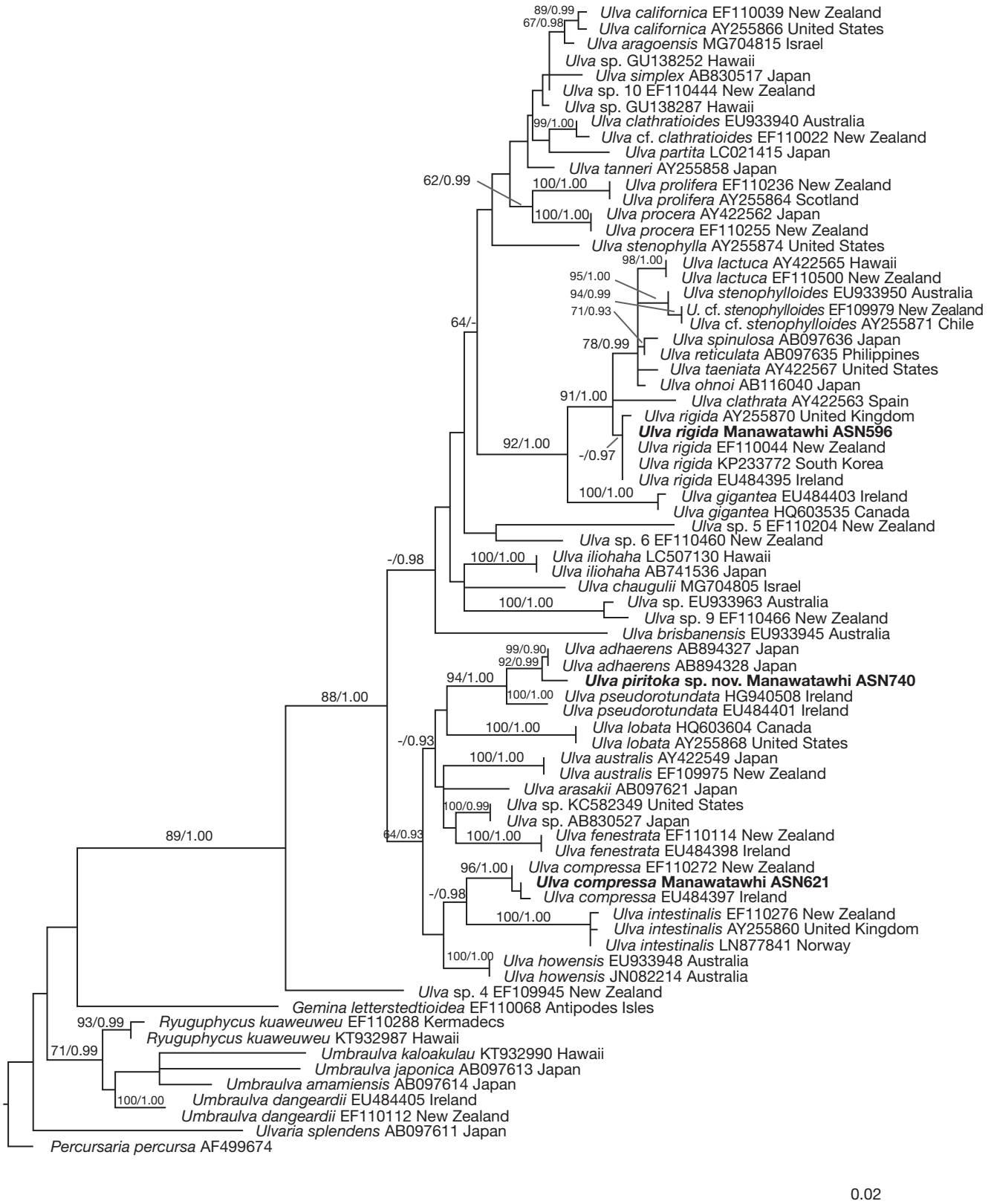


FIG. 3. — Phylogenetic tree inferred by Maximum Likelihood analysis from partial *rbcL* sequences of Ulvacean species. Numbers above lines indicate ML bootstrap support values (BS) and Bayesian posterior probabilities (PP). BS values below 60% and PP values below 0.9 are not shown. Species names (reflecting current nomenclature; Guiry & Guiry 2021) are followed by GenBank/ENA accession numbers and origin of the sample (see Table 2 for references). New sequences are set in **bold**.

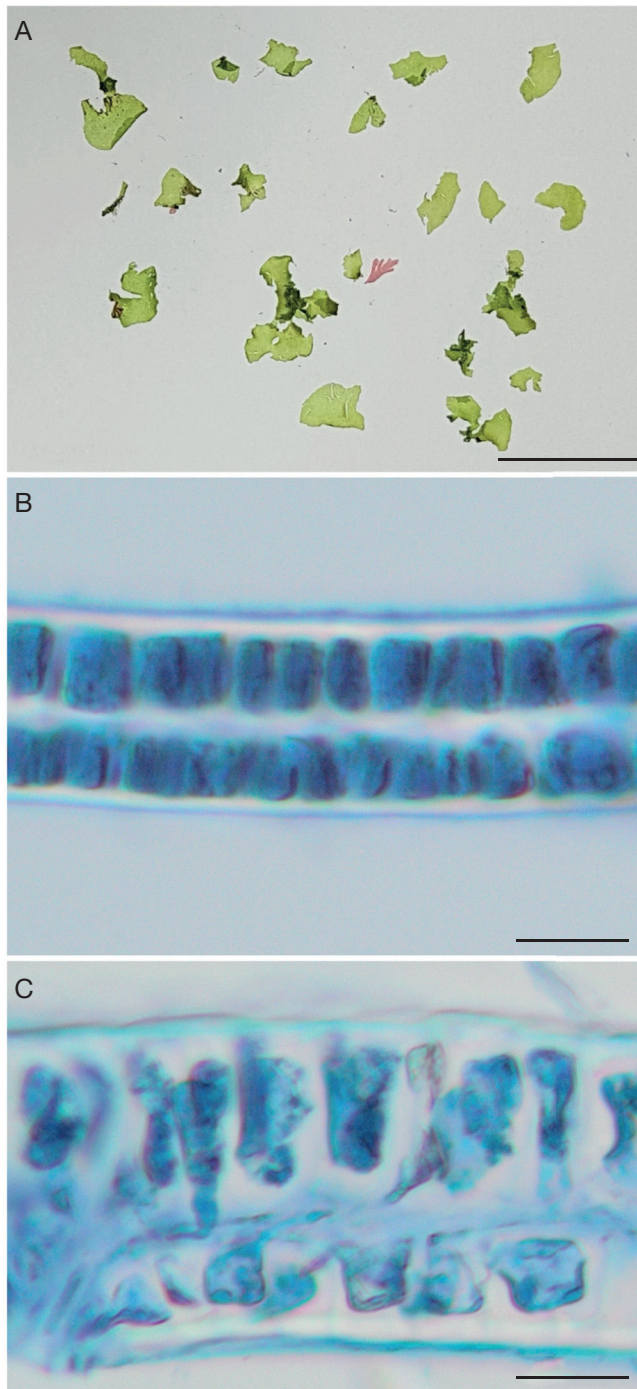


FIG. 4. — **A**, Holotype *Ulva piritoka* Ngāti Kuri, Heesch & W.A.Nelson, sp. nov.; **B**, section through distromatic blade; **C**, section in region of rhizodal clump showing deeper adaxial cell layer and rhizoids arising from cells of both thallus layers. Scale bars: A, 2 cm; B, C, 50 µm

be present in a lineage either by descent, or through a *de novo* insertion. The *U. adhaerens* intron is the only Group II intron identified so far in the *rbcL* of an *Ulva* species, although these introns have been observed in other Ulvophycean taxa (e.g., *Bryopsis maxima*, *Bryopsis plumosa*, *Codium fragile*, *Codium lucasii*, *Caulerpa okamurae*, *Caulerpa racemosa*; Hanyuda *et al.* 2000). The *U. adhaerens* intron contains a large open reading frame identified as a putative reverse transcriptase and

intron maturase (Matsumoto & Shimada 2015), supporting the hypothesis that this intron represents a relatively recent insertion into that lineage.

There are no examples to our knowledge of an Ulvophyceae taxon which shows intra-specific variation in the presence/absence of a Group II *rbcL* intron. Hanyuda *et al.* (2000) identified two varieties of *Caulerpa racemosa* which differed in the presence of a Group II intron in the *rbcL* gene: the intron was present in material identified as *Caulerpa racemosa* var. *clavifera* f. *macrophysa*, but not in specimens of *Caulerpa racemosa* var. *peltata*. However *Caulerpa racemosa* var. *peltata* is now regarded as a synonym of *Caulerpa chemnitzia* (Esper) J.V.Lamouroux (Guiry & Guiry 2021), and so this is not an example of intra-specific variation, but of intra-generic variability. In view of this we regard the presence of a Group II *rbcL* intron in *Ulva adhaerens*, but not in *Ulva piritoka* Ngāti Kuri, Heesch & W.A.Nelson, sp. nov., as supporting our hypothesis that they are best regarded as separate species.

The collaboration between Ngāti Kuri and taxonomists in naming the biota of Manawatāwhi acknowledges Ngāti Kuri as kaitiaki. Naming our world is central to the Indigenous movement towards further decolonisation of systems of power and marginalisation (Smith 2012). This collaboration within the study of algal taxonomy mobilises and articulates Ngāti Kuri autonomy within the Ngāti Kuri rohe, and works to enable the flow of knowledge, language, values and principles between taxonomic scientists and iwi. Ngāti Kuri knowledge-holders have developed a template that consists of kupu (Māori words) that can be used to describe and name biota within their rohe. The name *piritoka* was chosen to symbolise the way in which the small macroalga holds steadfast to rocks and withstands the constant ebb and flow of ocean currents. *Ulva piritoka* sp. nov. is small and yet robust.

Many *Ulva* species are extremely difficult to distinguish in the field either morphologically or based on habit or habitat. However, this new species of *Ulva* has a distinctive prostrate habit, and its attachment by scattered clumps of rhizoids is a morphological feature enabling it at present to be distinguished anatomically from other *Ulva* species in the New Zealand region.

The discovery at Manawatāwhi of two other species of *Ulva*, *U. compressa* and *U. rigida*, identified by molecular sequence data, raises a number of questions about their status. Both of these species were originally described from Europe (Guiry & Guiry 2021) and are currently regarded as non-indigenous in the New Zealand context (Neill & Nelson 2019).

The intertidal species *Ulva compressa* is reported to have a global distribution, and displays highly variable morphology (Heesch *et al.* 2007; Steinhagen *et al.* 2019). It is known as a hull-fouling species, tolerant to a wide range of environmental conditions, and capable of growing and reproducing rapidly (Blomster *et al.* 1998; Schaffelke *et al.* 2006; Ogawa *et al.* 2013, Steinhagen *et al.* 2019). Within mainland New Zealand, *U. compressa* has a wide geographical range, forming one of the most commonly collected species during national surveys of *Ulva*, always reported from intertidal sites, and with records from the North, South, Chatham and Stewart Islands, sug-

gesting that it naturalised some time ago (Heesch *et al.* 2007, 2009). No sequence data are available from type material of *U. compressa*. Described in 1753 by Linnaeus, Hayden *et al.* (2003) listed the type locality as “Bognor, Sussex, England?” and the Lectotype (epitype) as Dillenius (1742: pl. 9, fig. 8). Genetic data place the specimens from New Zealand (both mainland and Manawatāwhi) in a clade with specimens from Ireland, Canada, Japan and Australia, a distribution that strongly suggests human-mediated distribution.

In the survey of New Zealand *Ulva*, *Ulva rigida* was found on relatively few occasions. It occurred from the south of North Island (Wellington), around the South Island and on Stewart Island at both intertidal and subtidal sites, with most specimens collected from harbours and embayments rather than from the open coast (Heesch *et al.* 2007). The sequence data from the Manawatāwhi specimen place it in a clade with specimens from South Korea, Ireland and the United Kingdom, a distribution that strongly suggests that this species is not indigenous to Manawatāwhi.

The criteria used to evaluate whether species are native or non-indigenous (known or suspected to have been introduced as a result of human activities) include evidence of historical introductions, disjunct geographical distributions, whether the species is restricted to artificial substrates and/or habitats that coincide with potential vectors (e.g. shipping routes or areas of high shipping traffic), and lack of genetic diversity indicative of founder populations (Adams 1983; Nelson 1999a; Inglis *et al.* 2006; Heesch *et al.* 2007). However, the case of *Ulva pertusa* Kjellman illustrates the limits of using the current distribution in pristine vs human-influenced habitats as an indicator for native vs. introduced status and emphasises the necessity for examining genetic data. In their biogeographic treatment of Ulvaceae in New Zealand, Heesch *et al.* (2009) concluded that *U. pertusa* was native in New Zealand, as it was found to be one of the most wide-spread species occurring in harbours as well as in pristine habitats well away from major vessel traffic. However, Hanyuda *et al.* (2016) demonstrated that the genetic diversity of this species was much higher in Japan compared to other regions outside southeast Asia, including New Zealand. They concluded that *U. pertusa* is native in Japan, from where it was originally described (Kjellman 1897), and that it spread from there to other Pacific regions. Comparisons of sequence data showed it to be identical to *Ulva australis* Areschoug described from Australia (Areschoug 1854; Couceiro *et al.* 2011; Hanyuda & Kawai 2018). That the latter species was described even earlier than *U. pertusa*, indicates that the spread of this entity must have happened some time ago. Following the rules of the International Code of Nomenclature for algae, fungi, and plants regarding the priority of older names (Turland 2019), the name *U. australis* is the earlier and correct name for this species, which is recognised as native in Japan, but introduced to Australasia (Kirkendale *et al.* 2013; Hanyuda & Kawai 2018; Neill & Nelson 2019).

How would non-native species of *Ulva* have reached Manawatāwhi? And do they pose a risk to native species on the islands? There are no wharves or permanent landing sites

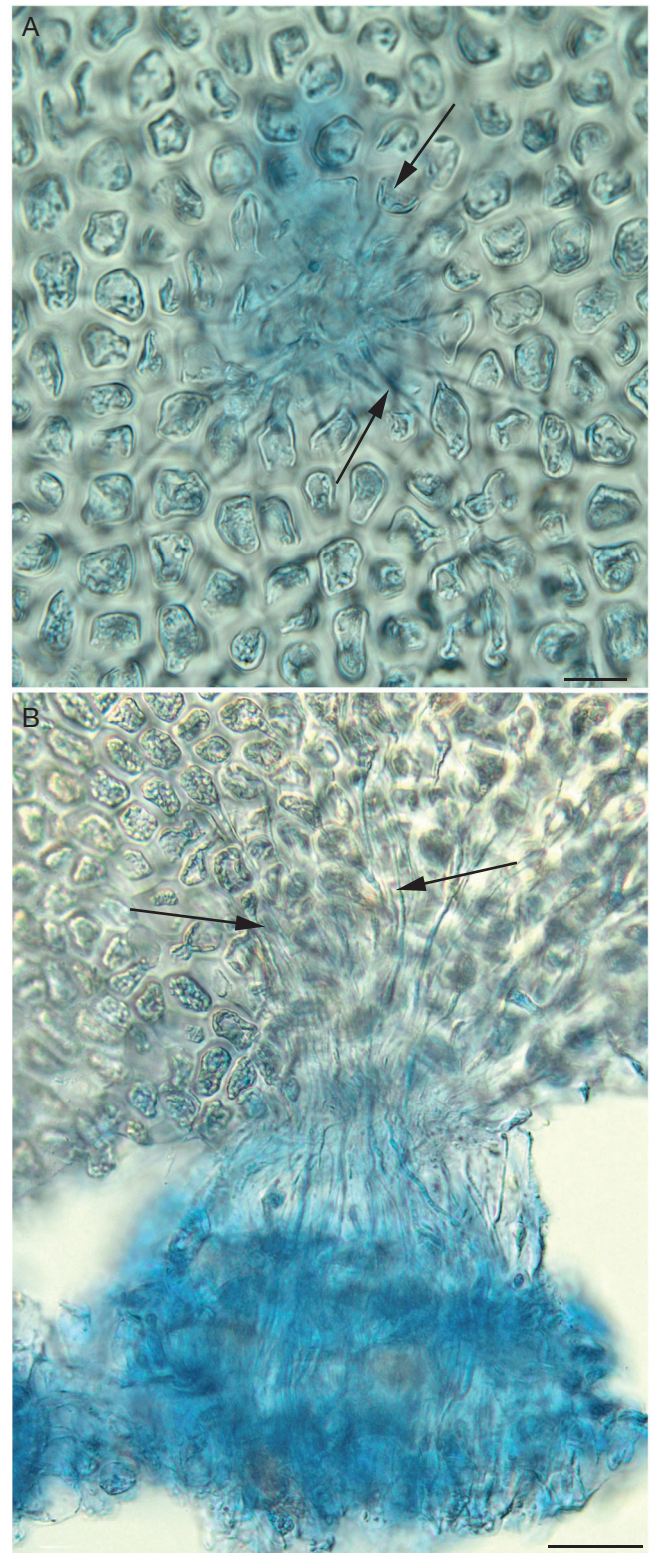


FIG. 5. — *Ulva piritoka* Ngāti Kuri, Heesch & W.A.Nelson, sp. nov.: **A**, surface view showing rhizoids extending from cells; **B**, rhizoidal clump from lower surface of thallus. Scale bars: A, 20 µm; B, 50 µm

on the islands – so direct transfer from the hull of a vessel at a mooring point is not possible. Species of *Ulva* are renowned for their reproductive output, producing both spores and gam-

etes. While it is unlikely that the small thalli of *Ulva* would survive floating long distances from mainland New Zealand sites or from material dislodged from the hulls of passing vessels, it is possible that floating debris/algal rafts could have been colonised by *Ulva* spp. and then washed ashore on the islands. Rafting is a known pathway for the distribution of marine species (e.g. Thiel & Gutow 2005; Thiel & Fraser 2016). Neither *U. compressa* nor *U. rigida* appeared to be abundant on the islands at the time of collection, nor were they over-growing other species.

Understanding the impact of non-indigenous species in marine environments is complex and is challenged by lack of data about marine NIS. The impact of marine NIS has been evaluated for only a very small fraction of species (Ojaveer *et al.* 2015), therefore negative impacts on human welfare (e.g. loss of ecosystem services, competition with valued native species, etc.) and economics also remain undetermined. There is little awareness of – and funding for – scientific studies that address this knowledge gap. Further investigation of Ulvaceae at Manawatāwhi is warranted to better understand the distribution of species, both seasonally and around this unique island group. Given the very high levels of endemism in the marine biota of Manawatāwhi, it is important that these islands are protected, and preventable vectors of potentially invasive species are excluded.

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