Marine Biology (2021) 168:47
https://doi.org/10.1007/s00227-021-03853-8

SHORT NOTES

# Pathogen inferred to have dispersed thousands of kilometres at sea, infecting multiple keystone kelp species

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Received: 25 November 2020 / Accepted: 19 February 2021 / Published online: 18 March 2021


## Abstract

Protistan pathogens have been found to infect populations of some large brown macroalgae. Infection could reduce the ability of macroalgae to withstand hydrodynamic pressures through weakening tissues and reducing flexibility. Widespread mortality of macroalgae if disease outbreaks were to occur could have important flow-on consequences for biodiversity and ecosystem function. Recent discoveries of the protistan pathogen *Maullinia* infecting the ecologically keystone southern bull kelp *Durvillaea* in Chile, Australia, and on Marion Island, raise the possibility that this pathogen is dispersing across ocean basins with buoyant hosts. To determine whether *Maullinia* also infects southern bull kelp in New Zealand, samples of gall-like tissue from *Durvillaea antarctica*, *D. poha*, and *D. willana* were collected from intertidal sites, and genetic analyses (sequencing of partial 18S rRNA) carried out. *Maullinia* infections were detected in all three species of *Durvillaea*. Phylogenetic analyses show a close relationship of New Zealand *Maullinia* to *M. braseltonii* previously detected in Chile and on Marion Island. Based on its genetic similarity to distant lineages and its presence on buoyant hosts that have been shown to drift long distances at seas, we infer that *Maullinia* has dispersed across the Southern Ocean through rafting of infected bull kelp. Understanding the capacity of pathogens to disperse across oceans is critical part of forecasting and managing ecosystem responses to environmental change.

## Introduction

Pathogens can have a major effect on ecosystem processes, and can exercise controls on populations through reducing the biomass and abundance of species, influencing the phenotypes of hosts, and altering species interactions (Price et al. 1986; Harvell et al. 2002; Groner et al. 2016; Fischhoff et al. 2020). Despite this, implications of disease have been understudied by ecologists relative to other biotic interactions (Campbell et al. 2014).

Responsible Editor: K. Bischof.

Reviewers:undisclosed experts.

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Parasites and pathogens are common in macroalgae, and whilst not all diseases will go on to disrupt ecosystem processes (Harley et al. 2012; Groner et al. 2016), when foundational species such as macroalgae are disrupted, it can have disproportionate impacts which cascade through trophic levels and alter habitat functioning (Harvell et al. 1999; Schiel 2006; Cohen et al. 2018). Such impacts are of particular concern in marine ecosystems where high levels of connectedness can facilitate rapid spread of pathogens over large distances (McCallum et al. 2003). Dispersal to new areas is likely to result in novel contact between the pathogen and the host, which could have serious consequences if the hosts have little or no resistance to the unfamiliar pathogen (Harvell et al. 2002; Cohen et al. 2018). Climate change is predicted to exacerbate the problem, through expanding pathogen ranges and making hosts more susceptible to infection through increased stress (Campbell et al. 2011; Kumar et al. 2016; Cohen et al. 2018). Early monitoring in combination with long-term data collection, including assessing disease prevalence, is essential to enable us to effectively respond to and manage disease outbreaks through understanding how host–pathogen interactions vary with climate

change and extreme events (Harvell et al. 2002; Burge et al. 2014; Groner et al. 2016).

*Maullinia* is an intracellular, protistan pathogen genus first described just 20 years ago when it was found on filamentous brown algae in Chile (Maier et al. 2000). Thus far, relatively little research has been carried out to understand the ecology of this pathogen, and the potential impact it could have on macroalgal communities. *Maullinia* has been found across the Southern Hemisphere, in Chile, the Falkland Islands, sub-Antarctic islands, and Australia on both filamentous brown algae and on southern bull kelp species (Maier et al. 2000; Goecke et al. 2012; Blake et al. 2017; Murúa et al. 2017). *Maullinia* can cause yellowish galls, between 0.5 and 4.0 cm in size (Goecke et al. 2012; Blake et al. 2017; Murúa et al. 2017) to form on southern bull kelp blades. Additionally, *M. ectocarpii* has been found to infect gametophytes of kelp species *Macrocystis* and *Desmarestia*, which could disrupt the life cycle of these keystone kelp species, particularly in a commercial context (Maier et al. 2000). Southern bull kelp (*Durvillaea*) are large and ecologically important keystone species occupying intertidal and shallow subtidal zones (Fraser et al. 2020). To withstand the wave forces in these dynamic environments, *Durvillaea* species are highly flexible and strong (Kelly and Brown 2000). The formation of galls on the blades of *Durvillaea* could reduce the kelps' elasticity and flexibility, which could affect their health and survival (Goecke et al. 2012). *Durvillaea* species provide refuge for understory species, and act as a substratum for various epiphyte taxa (Taylor and Schiel 2005). Some species host diverse invertebrate fauna in their holdfasts, many of which depend on the macroalgae for food and habitat. Additionally, stranded *Durvillaea* detritus is an important food source for marine and terrestrial fauna (Jaramillo et al. 2006; Dufour et al. 2012). These foundational species are essential for the healthy functioning of intertidal ecosystems in the cool-temperate Southern Hemisphere, as well as having important economic and social roles in aquaculture (Murúa et al. 2017).

The *Durvillaea* genus includes three buoyant species, whose thalli contain a gas-filled honeycomb structure (Fraser et al. 2020). This trait has promoted long-distance dispersal of *Durvillaea* species such as *D. antarctica*, which has been found washed up on coasts thousands—and even tens of thousands—of kilometres away from known source populations (Moore and Cribb 1952; Fraser et al. 2011, 2018; Waters et al. 2018). These buoyant species are an important mechanism for the dispersal of coastal taxa, as they can transport other organisms with them, such as invertebrates, other algal species, and marine parasites (Thiel and Gutow 2005a, b; Fraser and Waters 2013). Emerging data showing a wide distribution of *Maullinia* across the Southern Hemisphere suggest that *Maullinia* might also disperse with these buoyant hosts. Research into the dispersal of *Maullinia* without host organisms is limited. The life cycle of *Maullinia* does include resting spores (Maier et al. 2000; Parodi et al. 2010; Goecke et al. 2012; Murúa et al. 2017), which may be able to survive for periods without the host (Neuhauser et al. 2011), but the extent of this is currently unknown, as is its ability to disperse on artificial substrata. Additionally, *M. ectocarpii* has been found to form cysts on sporangia of filamentous seaweeds (Maier et al. 2000), but there are no records of *M. ectocarpii* forming cysts on artificial substrata and dispersing in this way. Blake et al. (2017) found evidence that a *Maullinia* lineage on buoyant *Durvillaea* in Chile was indistinguishable from a lineage on buoyant *Durvillaea* on the distant sub-Antarctic Marion Island in the Indian Ocean, and that a lineage found on the filamentous alga *Ectocarpus* in Chile was closely related to lineages detected on non-buoyant *Durvillaea* in Australia, suggesting long-distance dispersal had recently occurred. Additionally, *Maullinia* prevalence differed with latitude, suggesting that environmental parameters affect the susceptibility of *Durvillaea* to infection (Blake et al. 2017).

New Zealand is a centre of diversity for southern bull kelp species, with several buoyant and non-buoyant species found in the region (Fraser et al. 2020). To date, however, *Maullinia* infections have not been recorded from New Zealand bull kelp populations. Given the evidence for long-distance dispersal of these marine pathogens around the Southern Hemisphere, we hypothesised that *Maullinia* would also be present in New Zealand. We tested this hypothesis using targeted sampling of tissue from three sympatric but ecologically and morphologically distinct *Durvillaea* species in New Zealand (the buoyant species *D. antarctica* and *D. poha*, and the non-buoyant species *D. willana*), followed by genetic sequencing to test for presence of the pathogen.

## Methodology

### Sampling

Sampling was conducted at eight sites on the south-east coast of the South Island, New Zealand, and one site on the North Island near Wellington (Fig. 1). The majority of the sampling occurred between February and March 2020 with the exception of Taieri Beach and Island Bay which were sampled in March and December 2019, respectively, in the intertidal zone of rock platforms (Appendix S1). *Durvillaea poha*, *D. antarctica* and *D. willana* were visually examined for signs of any pathogenic infection such as lesions or galls. 123 tissue samples from individual *Durvillaea* species were collected from infected kelp to test the presence of *Maullinia* via genetic analysis. Samples were either air-dried on a clean paper towel after initial desiccation in high-concentration

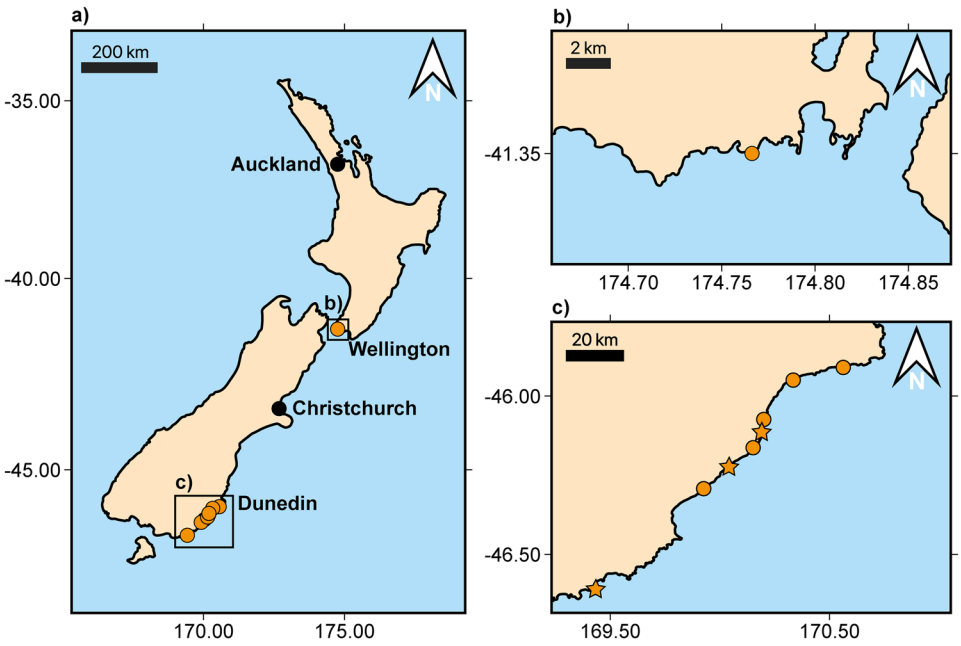


**Fig. 1** Sites in New Zealand where field sampling was conducted in **b** one site in the North Island and **c** eight sites in the South Island. Stars in panel (**c**) represent sites where *Maullinia* was confirmed from *Durvillaea* hosts

ethanol, or air-dried in an oven at 50 ºC for several hours, and then stored over silica gel beads.

## Genetic analysis

All 123 samples had DNA extracted and underwent PCR. DNA extraction and PCR followed methods described in Blake et al. (2017). Small (< 2 mm) pieces of infected, dried kelp tissue were excised using a scalpel sterilized with bleach and ethanol, and DNA was extracted using the standard Chelex® protocol (Walsh et al. 1991). Extractions were diluted 1:100 in MilliQ water to reduce the likelihood of alginates inhibiting PCR. PCR amplification was conducted in a 20 µl solution, comprising 12.9 µl of MilliQ water, 0.5 µM each of forward and reverse primer (Mau2F and Mau9R: Goecke et al. 2012), 4 µl of MyTaq Red Reaction buffer, 0.1 µl of MyTaq Red DNA Polymerase (Bioline), and 1 µl of the diluted DNA extraction. The primers amplified part of the 18S nuclear ribosomal gene. PCRs were run in an Eppendorf Mastercycler using a touchdown PCR protocol: 96 ºC for 4 min initial denaturation, followed by two cycles of 96 ºC for 25 s, 65 ºC for 25 s and 72 ºC for 1.5 min followed by two cycles each with a primer annealing temperature of 60 ºC and 58 ºC and finally 30 cycles with a primer annealing temperature of 54 ºC and a final slope of 72 ºC for 10 min (Goecke et al. 2012). PCR products (~ 1200 bp in size) were purified using gel purification via a MEGAquick-spin™ plus fragment DNA purification kit (iNtRON). Some samples also showed amplification of a smaller fragment (~ 300 bp); sequencing revealed that these amplicons were from the host (BLAST results showed close match to a part of the 18S marker amplified from *Durvillaea*), suggesting that the primers can sometimes anneal to New Zealand bull kelp DNA. By gel purifying amplicons, we were able to target the pathogen rather than the host. For samples where *Maullinia* sequences were confirmed, COI sequences of the host were subsequently obtained following methods in Fraser et al. (2009) to verify host identification, as *D. poha* and *D. antarctica* can sometimes be misidentified in the field. Sequencing was carried out using the forward primer by the University of Otago's Genetic Analysis Services (Otago, New Zealand), using an Applied Biosystems 3730xl capillary sequencer (Thermo Fisher Scientific).

## Phylogenetic analysis

Sequences were aligned, and ambiguities assessed by eye using Geneious Prime version 2020.1.1 (Kearse et al. 2012). Sequences were trimmed to 764 bases to remove poor-quality sequence tails. Original sequences from Blake et al. 2017, and published sequences from known *Maullinia* species (*M. braseltonii*: GenBank Accession JX163857, and *M. ectocarpii*, Accession AF405547) were aligned with new sequences from this study. A mid-point rooted ML tree was built using PhyML (Guindon et al. 2010) via a TRN + I model (best model as assessed by the AICc of jModeltest2: Darriba et al. 2012), with the proportion of invariable sites set at 0.809.

# Results and discussion

The protistan pathogen *Maullinia* was confirmed from three bull kelp species in New Zealand: the buoyant *D. antarctica* (one individual) and *D. poha* (three individuals), and the

solid-bladed *D. willana* (one individual) (Table 1). *Maullinia* was detected at three intertidal sites on the South Island across a coastal distance of > 70 km (Fig. 1) suggesting the pathogen might be widespread, albeit probably at low prevalence, in southern New Zealand. Two sequences of *Maullinia* were detected. The first was detected from one individual of *D. willana*, a non-buoyant bull kelp species, and was identical to the most common sequence of *M. braseltonii* detected from buoyant bull kelp in Chile by Blake et al. (2017), lineage MC1 (GenBank Accession MF872446) (Fig. 2). The second sequence was detected from one individual of *D. antarctica* and three individuals of *D. poha*—the two buoyant hosts—and were identical across all sites and samples to each other, but the sequence had not been previously detected elsewhere (GenBank Accession MW131091). This lineage is most likely also *M. braseltonii*, as it differed from the other *D. willana*-associated sequence at only five out of 764 nucleotide sites (< 1%; four transitions and two transversions). Both sequences found in this study were highly similar to sequences of *M. braseltonii* detected from buoyant species *D. incurvata* (recently split from *D. antarctica* (Fraser et al. 2020)) in Chile, and *D. antarctica* in the sub-Antarctic (Blake et al. 2017). That two lineages were detected could indicate multiple past introductions, or perhaps evolution of the pathogen driven by different host tissue types (buoyant, inflated blades versus non-buoyant, solid blades); a larger scale study could, in future, aim to test such hypotheses.

The discovery of *M. braseltonii* on bull kelp in New Zealand and its genetic similarity to geographically distant lineages suggests that *M. braseltonii* could have arrived through long-distance rafting of infected, buoyant kelp, either dispersing from Chile or sub-Antarctic islands to New Zealand, or vice versa. Further sampling could help to clarify the direction of travel. Our finding supports previous inferences of long-distance dispersal of marine pathogens via rafting with buoyant macroalgae (Fraser and Waters 2013; Blake et al. 2017). Blake et al. (2017) found *M. ectocarpii* in Australia on bull kelp taxa *D. potatorum* and *D. amatheiae*, so we might have expected to find *M. ectocarpii* in New Zealand (geographically relatively close to Australia), but these solid-bladed *Durvillaea* species are non-buoyant and thus have limited dispersal opportunities (Fraser et al. 2020; Hay 2020). In contrast, *M. braseltonii*—which as we show here can infect both buoyant and non-buoyant *Durvillaea*—has now been shown to have a wide geographic range, infecting bull kelp in Chile, Marion Island (sub-Antarctic Indian Ocean) and New Zealand—locations separated by thousands of kilometres of ocean. *Maullinia braseltonii* might also be a more generalist pathogen than *M. ectocarpii*, as the same strain of *M.* braseltonii was found to infect both *D. antarctica* and *D. poha*. In contrast, strains of *M. ectocarpii* appear to be host specific in Australia (Blake et al. 2017). The capacity of the pathogen to infect several host species, including both buoyant and non-buoyant taxa in addition to filamentous alga previously found to be infected by *M. ectocarpii* (Maier et al. 2000), shows that *Maullinia* is a versatile and generalist pathogen.

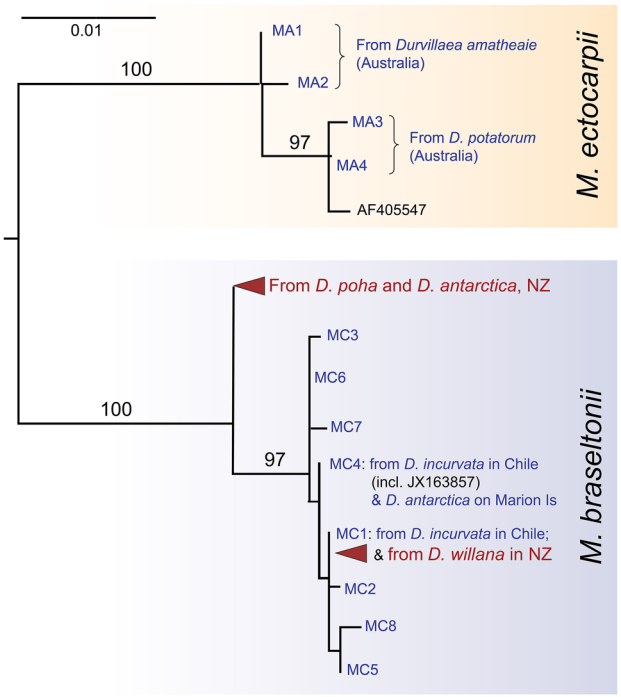


**Fig. 2** Maximum likelihood phylogeny of published and new *Maullinia* partial 18S data. The samples from New Zealand (this study) group with previously detected sequences from southern bull kelp from Chile and the sub-Antarctic. Blue text indicates data from Blake et al. (2017) (code MA refers to *Maullinia* detected in Australia, and code MC refers to strains collected from Chile, in that study), and red text indicates sequences from this study. The phylogeny is mid-point-rooted, with bootstrap values > 90% shown

**Table 1** *Maullinia* sequences and host *Durvillaea* species with associated GenBank accession numbers and site locations

| *Maullinia* sp. | Host *Durvillaea* sp. | GenBank accession number | Number of confirmed infections | Sample site |
|---|---|---|---|---|
| *M. braseltonii* | *D. willana* | MF872446 | 1 | Akatore |
| *M. braseltonii* | *D. antarctica* *D. poha* | MW131091 | 4 | Toko Mouth and Tautuku Peninsula |

From previous reports of *Maullinia* infection of bull kelp, we expected to find yellowish galls to indicate the pathogen's presence (Goecke et al. 2012; Blake et al. 2017). None of the bull kelp populations surveyed, however, showed obvious, large galls—instead showing only minor blemishes on host tissue—suggesting that galls are not always indicative of *Maullinia* infections. There might, however, be some seasonality in gall development, or environmental factors that influence the prevalence and manifestation of infections (Schade et al. 2016; Ford et al. 2018; Honjo et al. 2020). With the potential of disease outbreaks to have major impacts on population health and viability, further research is urgently needed to better understand the characteristics of this relatively newly discovered (Goecke et al. 2012), but apparently highly dispersive (Blake et al. 2017; this study) kelp pathogen.

*Maullinia* prevalence on bull kelp hosts has been found to vary with latitude and the associated environmental parameters (Blake et al. 2017). Infection prevalence increased towards higher latitudes in both Chile and Australia, which could be due to increased population density in southern parts of *Durvillaea*'s range, or it could be that the *Maullinia* pathogen is more prevalent in colder waters (Blake et al. 2017), which may mean that increased temperatures could counteract the virulence of this pathogen (Blake et al. 2017). However this could be offset by physiological stresses caused by higher temperatures increasing organisms' susceptibility to disease (Case et al. 2011; Campbell et al. 2011; Beattie et al. 2018; Thomsen et al. 2019). Predicting how environmental change will affect the prevalence and impacts of *Maullinia* on *Durvillaea* is, therefore, currently difficult. *Durvillaea* species comprise a large proportion of the macroalgae biomass in coastal ecosystems in New Zealand (Thomsen et al. 2019; Hay 2020) and it would be devastating for nearshore marine communities if a disease outbreak were to significantly reduce the biomass of these species (Taylor and Schiel 2005; Jaramillo et al. 2006; Dufour et al. 2012; Murúa et al. 2017). Previous mortality events of *Durvillaea* have led to the increased spread of the highly invasive kelp *Undaria pinnatifida* (Thomsen et al. 2019), and the replacement of *Durvillaea* with this species would change the character and functioning of the ecosystem (Stuart 2004; Russell et al. 2008).

Understanding the controls of pathogen distributions is essential for monitoring and managing future disease outbreaks. Further assessment of macroalgal populations in New Zealand and elsewhere will be important to determine the virulence and potential risks this pathogen poses for coastal communities.

**Supplementary Information** The online version contains supplementary material available at https://doi.org/10.1007/s00227-021-03853-8.

**Acknowledgements** We thank Dave Craw, Felix Vaux and Graham Wallis for assistance in the field, Aled D. Evans for assistance with creation of the maps, and Jane A. Catford for facilitating this collaboration. CIF was supported by a Rutherford Discovery Fellowship from the Royal Society of New Zealand (RDF-UOO1803). AM was supported by the Natural Environmental Research Council [Grant number NE/L002531/1] and a School of Biological Sciences Studentship at the University of Southampton. We would also like to thank the reviewers for their constructive feedback of the manuscript.

**Data availability** The novel sequence detected in this study has been made publicly available by deposition in GenBank, Accession MW131091.

## Declarations

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethical approval** All applicable international, national and institutional guidelines for sampling of organisms for the study have been followed.



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