Marine wood borers in New Zealand: an interdisciplinary study of their origins, impacts and management

A thesis

submitted in partial fulfilment

of the requirements for the degree

of

Masters of Science in Biology

in Biological Sciences

at

The University of Waikato

by

COURTNEY A. RAYES

THE UNIVERSITY OF
WAIKATO
Te Whare Wānanga o Waikato

2014

Abstract

Non-indigenous marine species are a major concern worldwide. For some species, insufficient historical and biogeographical data can leave their origin and patterns of dispersal difficult to determine. Among such species are marine wood borers. This thesis uses an interdisciplinary approach, combining both historical and biological methods, to address marine borer impacts, management attempts, and their status in New Zealand.

This research had two key components. Firstly, a historical review sought to improve the understanding and awareness of the historic impacts and responses to borers, with particular reference to New Zealand between 1850 and 1930. Marine wood borers have had profound impacts throughout history, responsible for significant structural and economic damage to wooden ships and marine infrastructure globally. In New Zealand, trade and economy played an important role in providing both the transportation vectors and infrastructure for marine wood borers to inhabit. Ongoing trialling of timber alternatives and chemicals for the preservation of infrastructure followed, with little success until the introduction of ferro-concrete in the early 1900s. When considered in a global context, the New Zealand case study of borer impacts and management attempts highlights their significant role in environmental history.

Mitochondrial DNA (COI) sequence analyses were used to examine the questionable invasion histories and status of common marine wood borers in New Zealand. It has been assumed that many marine wood borers invaded New Zealand via wooden ships. However, these purported introductions are historic, and the specific origins of many species are unclear. Species from three families and two phyla were collected around the North Island, New Zealand; Teredinidae (Bivalvia: Mollusca), Sphaeromatidae and Limnoriidae (Isopoda: Arthropoda).

Low levels of genetic divergence (0-2%) were found among the New Zealand populations of two species, *Limnoria quadripunctata* and *Sphaeroma quoianum*, suggesting a non-indigenous status. *Limnoria quadripunctata* also showed a close genetic affinity to populations in Chile, supporting a non-indigenous status, with its widespread distribution in New Zealand explained by multiple introductions. For *Lyrodus pedicellatus*, a lack of genetic affinity to conspecifics sequenced elsewhere (France), greater genetic diversity compared to the native *Bankia australis*, and evidence of population structuring among New Zealand locations, suggested *L. pedicellatus* may be native to New Zealand. *Lyrodus pedicellatus* from New Zealand was highly divergent (>20%) from global *L. pedicellatus* populations, suggesting that either identifications of specimens on global databases are incorrect, or the New Zealand species represents a morphologically undescribed cryptic congener. In conclusion, COI sequences provided a useful tool in elucidating the status of marine wood borers in New Zealand, and highlighted a need for taxonomic resolution of some species.

Collectively the two chapters illustrate the knowledge gaps and lack of recognition surrounding marine wood borers, globally and in New Zealand. This research provides an extensive understanding of their significant historical role in marine environmental history and assists in re-evaluation of their current native or non-indigenous status in New Zealand.

Acknowledgments

I would like to start with a big thank you to all my supervisors, without their guidance and support this thesis would not have been possible. To Dr Ian Duggan, as my primary supervisor you have been a huge support throughout the entire process. Available at all times to discuss ideas, and even with the new addition to your family you still managed to make time to edit my writing at all hours of the night. To Dr Ian Hogg for your direction in the genetics lab, for answering the many questions I had, and for the time set aside for editing my work. To Dr James Beattie, thank you for introducing me to the new perspective of environmental history and mentoring me through the historical writing process. My research was also financially supported through my supervisors, which is greatly appreciated.

To my Nan and Poppa, thank you for the assistance and use of tools in the construction of my wooden ladders, and also for feeding and accommodating me on numerous trips home. To Hannah, McKenzie, Sianne and Tom, you were fantastic field assistants, and were great company in the hours of driving around the North Island. I really am grateful for all of you giving up a week of your time to assist, and for showing unwavering enthusiasm while extracting the borers. Thank you to Gemma, Jeremy and Mandy who were also available for the day trips to Raglan and Tauranga to attach or retrieve the last wooden ladders. A big thank you to Sophie, Seb, Mandy, Paul, Margot and the family, for hosting us on fieldwork - even when we arrived and departed at ridiculous hours to make the tides.

To the Waikato lab crew, in particular, Kristi, Gemma and the Steve's, who answered all my queries and were great company in general. A special thanks to Kristi who taught me all of the lab protocols, analyses, and was always available to assist with any issues. Thank you to my amazing editors who were very helpful in the writing of my thesis: Sophie, Seb, Mandy, and Sianne. Without you there would be no way for me to know if a non-science person could understand it.

Thank you to all of the people I have received ongoing support from throughout my masters and the previous years of study. To my sisters, McKenzie for the almost daily phone calls just to keep updated, and Morgan for all her motherly concerns resulting in free petrol and a garage to store my life possessions. Thank you to Uncle Mark and Aunty Angela for supplying me with large amounts of food. A big thank you to those who made the years of study a lot easier, Kathy for the assistance in my very first year of study, Laura for the encouragement, and Lou and Norm for all your helpful advice, great company and a place to stay if ever I needed. Thank you also to Dad and Carol for amongst other things automatically paying my car insurance without knowing!

A big thank you to Mandy and the Scott-Simmonds family for providing the respite of numerous fishing and diving trips on my weekends off, an amazing place to stay at the mount, and all the support I could ever ask for. Last, but not least, to Tom for putting up with my detailed explanations of shipworms and gribbles, and for the much needed reprieve throughout the two years.

It is not one person but all of you collectively, that made possible the completion of this thesis - I cannot thank you all enough.

Table of Contents

List of Figures

List of Tables

Chapter I

Thesis Introduction

Globally, humans have been responsible for the transportation, introduction and establishment of a variety of marine species (Roman and Darling 2007). Following establishment, many species have had devastating ecological and economic impacts (Ruiz and Carlton 2003). Amongst such species are marine wood borers, which are accountable for significant structural damage and economic loss (Davidson and de Rivera 2012). Humans have facilitated the movement of non-indigenous marine species around the world, with shipping the predominant transportation vector (Fofonoff et al. 2003). In recent times ballast water and hull fouling have been important mechanisms for the movement of biota by ships. However, historically (pre-1900) solid ballast and hull fouling were significant, with wooden vessels also providing a vector for marine wood borers (Carlton and Hodder 1995; Fofonoff et al. 2003; Hayden et al. 2009).

Marine wood borers are from two taxonomic classes and represented by three key families, Teredinidae (Bivalvia; Mollusca), Sphaeromatidae and Limnoriidae (Isopoda; Arthropoda), otherwise known as shipworms, pillbugs and gribbles (Miller 1926; Cragg et al. 1999; Paalvast and van der Velde 2011). The fundamental role timber has played in the construction of wooden vessels and marine infrastructure has subsequently provided borers with suitable substrates to inhabit. Furthermore, their movement has been mediated by humans, historically through wooden hull boring, and more recently in ballast water and wooden aquaculture materials (McKoy 1980; Hayden et al. 2009). Regardless of the numerous efforts to prevent borer damage, including material alternatives and various preservatives, a lasting method is yet to be discovered (Cookson 1986). The borer problem continues to remain a concern today with their ongoing expansion into new regions (Gregory 2010).

While borers are seen to have large adverse impacts, humans have only exacerbated these by providing the suitable habitats and vectors for transport. Moreover, from an ecological perspective, borers play a fundamental role in the break-down of woody debris in estuarine ecosystems (Santhakumaran 2003). The decomposition of woody debris also replenishes coastal and off-shore nutrients, utilized in pelagic foodwebs, and shapes the lower intertidal limits of mangrove forests (Simberloff et al. 1978; Cragg 1993; Svavarsson et al. 2002). Therefore, despite their destructive nature, borers also provide an ecologically important function within the marine environment.

The occurrence of adverse borer impacts to wooden vessels dates back to at least the second millennium BCE, with the infestation of wooden vessels in Egypt (Borojevic et al. 2010). Many seafarers documented borer damage along their journeys, and a considerable number of historic references detail their destructive nature (Elder 1856; Barnaby 1860; Morison 1942). Prior to the introduction and use of iron steamships in the 1860s, large numbers of references to borers focussed on their management with respect to wooden vessels, describing the careening and various preservative hull coating methods; more recently, marine infrastructure has become the focus (Thunberg 1796; Elder 1856; Barnaby 1860; Morison 1942). Amongst the most well-known borer references are the invasions of teredinids in the Netherlands around 1730 and San Francisco Bay 1914, where seawalls and wooden infrastructure were significantly destroyed, leaving millions of dollars worth of damage (San Francisco Bay Marine Piling Committee 1927; Paalvast and van der Velde 2011). Such examples illustrate the destructive potential of marine wood borers and highlight the need for a greater understanding of the vectors, pathways, invasion risk and management. As a whole it is clear borers played a significant role in marine environmental history, yet despite the prominence of borers around the world, there is a clear need for amalgamation of the scattered literature.

Currently many borer species are considered to have cosmopolitan distributions, and the historical nature of their dispersal makes determining their origins difficult. Thus, numerous species' origins remain unclear (Edmonson 1962; CABI 2013). Despite this uncertainty, many borer species have been assigned by inference a native or non-indigenous status within specific regions (Holthuis 1949; Cookson 1991; Cranfield et al. 1998; Johns 2010). However, a 'cryptogenic' status may be more fitting for most, as it better signifies their uncertain origins and the inability to distinguish between native and non-indigenous species (Carlton 1996). In order to improve the scientific understanding of marine wood borers, clarification of their current status is necessary.

All three of the borer families present taxonomic issues, leading to errors in identification and challenging the overall scientific understanding of each species, which relies on taxonomic precision (Edmonson 1962; Turner 1966; Paalvast and van der Velde 2011; CABI 2013). In recent years, studies have focussed on correcting taxonomic and systematic discrepancies by utilizing molecular genetics and examining patterns of genetic variation. Although analyses of mitochondrial DNA sequences have proven a good method to correctly identify borer species and recognise genetic differences between populations, its use has been limited to date (Santos et al. 2005; Nikula et al. 2010; Borges et al. 2012; Haye et al. 2012). Questionable invasion histories, particularly those of cryptogenic species, can also be analysed using DNA barcoding to examine population genetic structure, species diversity and taxon relationships, (Blakeslee et al. 2008).

New Zealand

New Zealand presents an ideal case study, with the presence of several native and non-indigenous marine wood borer species. Marine introductions to New Zealand are thought to have occurred since European colonization in the nineteenth century, and potentially prior to this with Māori settlers ca. 1300 (Hayden et al. 2009). Several studies have incorporated testable criteria for identifying introduced species, which resulted in a list of non-indigenous species in New Zealand by Cranfield et al. (1998). Included on the list are several marine wood borers. However, due to the questionable biogeography and historic data, such criteria can result in an unsystematic bias towards either a native or non-native status (Ruiz et al. 1997; Hayden et al. 2009; Gordon 2011). In particular, for New Zealand's marine wood borers the lack of acknowledgment of species presence prior to European arrival, unknown early date of introductions and 'probable' native ranges, has resulted in potentially unreliable inferences of their non-indigenous status (Cranfield et al. 1998). Furthermore, this lack of historic knowledge regarding introduced species leaves the possibility that species designated as native also potentially arrived through historic shipping routes, yet their current widespread distribution makes it difficult to distinguish them as non-indigenous (Hayden et al. 2009). For these reasons, several of New Zealand's marine wood borers currently present a cryptogenic status and are ideal candidates for genetic evaluation.

Past studies have described eight species of woodborers distributed amongst North Island sites, although some species were isolated to a single port (McQuire 1964; McKoy 1980). All of these studies are greater than 30 years old, and conducted sampling primarily in modern ports, leaving some historical shipping regions and other coastlines poorly represented (e.g. south eastern and far northern regions).

New Zealand has representatives from all three of the major wood boring families. Nine species of Limnoriidae are known from New Zealand, including two wood borers, *Limnoria quadripunctata*, which is widespread, and *Limnoria tripunctata*, found only in Auckland harbour. Both species are considered non-indigenous (Cookson 1991). *Limnoria quadripunctata* was first recognized in the Netherlands, although it is currently recognized around the globe and presents no certain origin (Holthuis 1949; Johns 2010). *Limnoria tripunctata* has a tropical cosmopolitan distribution, and as with *L. quadripunctata*, the timing of its introduction to New Zealand is unknown (Cranfield et al. 1998). Two new wood-boring Limnoriidae species were also discovered in 1989 from rotting wood off New Zealand's coast: *L. hicksi* and *L. reniculus*, although to date no further information on these species has been published (Schotte 1989).

Hurley and Jansen (1977) listed fifty Sphaeromatid species from New Zealand, although only two of these species are recognized as borers of wood. *Sphaeroma quoianum* was presumed to be native to New Zealand by the Invasive Species Specialist Group (2008), as listed in the Global Invasive Species Database, while it is considered non-indigenous in Johns (2010). New Zealand distribution studies have recorded this species in several North Island and northern South Island harbours (McQuire 1964; Hurley and Jansen 1977). The contrasting reports indicate a need for validation of the status of *S. quoianum* in New Zealand. A native species, *Sphaeroma laurensi*, is also listed as present in the east coast harbour of Gisborne, but no other records of this species have been recorded in New Zealand (Hurley and Jansen 1977).

The most recent studies on the distributions of New Zealand teredinids document five different species in the intertidal region around the North Island, New Zealand (McQuire 1965; McKoy 1980). Three species, *Lyrodus mediolobatus*, *L. pedicellatus* and *Nototeredo edax*, have an inferred non-indigenous status in New Zealand (Cranfield et al. 1998). On the other hand, *Bankia australis* and *Bankia neztalia* are considered native (McKoy 1980; Cranfield et al. 1998). Both *Lyrodus* species are globally widespread, with probable native ranges of tropical to temperate cosmopolitan; both are also present in numerous harbours around the North Island, New Zealand (McKoy 1980; Cranfield et al. 1998). The probable native range of *N. edax* is tropical Pacific and it is also known from several North Island harbours (Cranfield et al. 1998). Despite the inference of 'probable' native ranges for these species, there is no known specific origin or timing of introduction known. The two native species are widely distributed around North and South Island harbours in New Zealand (McKoy 1980). Despite the current lack of information or subsequent reporting of these species, also listed as present in New Zealand are native *Nausitora* spp. cf. *aurita* and *Uperotus clavus* (Campbell et al. 2009).

Thesis Outline

In this thesis I use and inter-disciplinary approach, combining both historical and biological methods, to address marine borer impacts, management, and their questionable native or non-indigenous status in New Zealand.

My first chapter explores the historical role and lasting presence of marine wood borers on a global scale, and then focuses specifically on borer extent, impacts, and societal response around New Zealand following Māori and European colonization. The main aim is to create a greater awareness of the significant role borers have played in the marine environment, through the synthesis of a diverse literature from scientific papers and newspaper articles, placing this information into context and making it more readily available. Furthermore, the historical review gives an in-depth analysis of connections between borer damage and historical port use around New Zealand. This knowledge of historical ports and past damage also provided the foundation for selecting the fieldwork sites for the following chapter, whereby ports could be selected to represent historically important shipping regions (and areas of historic damage) poorly represented in past studies. By incorporating history, this study also addresses economic and social drivers of potential borer introduction and spread, which is necessary to gain a greater scientific understanding of species presence and movement around the globe (Hayden et al. 2009).

The second chapter examines geographical distributions and genetic structuring and diversity of Limnoriidae, Sphaeromatidae and Teredinidae populations around the North Island, New Zealand. The main aim was to use genetics as a tool to better elucidate the status of borer species, as native or non-indigenous. Nucleotide sequencing of the mitochondrial gene, cytochrome *c* oxidase I (COI), has been shown to be successful for identifying and distinguishing between borer species, and provides insight into intra- and inter-specific diversity (Nikula et al. 2010; Baratti et al. 2011; Borges et al. 2012). Furthermore, studies in New Zealand have used the COI gene to examine genetic structuring of marine taxa with respect to geographical distributions (e.g., Hickey et al. 2009; Knox et al. 2011, Ross et al. 2012), and to clarify species' status (e.g., Stevens et al 2002). A number of coastal marine species show clear genetic structuring, influenced by oceanic currents and natural boundaries, including genetically divergent regions of the East Cape, Cook Strait and East/West coasts of the North Island (Ross et al.

2009). These past studies provide comparisons to determine whether the genetic structuring in borer species occurs in the same manner.

Collectively, the two chapters seek to address gaps in the literature and the lack of awareness surrounding marine wood borers, both globally, and specifically in New Zealand. Investigation into the significant historical role of marine wood borers, combined with genetic analyses, provides a broad understanding of the impacts, management attempts, and distributions of borer species, and helps to re-evaluate the native or non-indigenous status' of species by addressing the lack of biogeographical and historical data of borers around New Zealand. The historical review provides the foundation for scientific research, by establishing the connections between borer presence and historically important ports, allowing for comparison with their current distributions and status. Integrated studies such as this give an improved depth of analysis, reflecting on the why, how, when and where of borer presence and movement, which is necessary in achieving a greater scientific understanding of marine wood borers and their invasive potential (Ruiz and Carlton 2003; Repko 2008).

I have written the chapters as stand-alone papers for submission. As such there are stylistic differences between the two major components. The history chapter is written as a literature review for an environmental history journal, incorporating significant new perspectives on the social, cultural and economic aspects associated with the movement of borers around the globe. This section also relies mainly on information gleaned from online databases of colonial newspapers, New Zealand statistics, and history books. The science chapter is written in the standard scientific paper format (abstract, introduction, methods, results, discussion and conclusion), reporting on experimental analyses and is based around specific hypotheses. The source material for the science chapter came from biological field sampling, genetic laboratory analyses, and peer reviewed articles published in scientific journals. Another key stylistic difference between the chapters is the use of active (history chapter) and passive (science chapter) voices. Active voice is most commonly used in historical writing to produce stronger and smoother sentences, and emphasise who or what is responsible for an action (Jenkins 2003). However, a passive voice is important in science for clarity, and changes the focus to the objects of the sentence rather than the scientists themselves (Knight 2003). Both chapter's referencing systems also adhere to the guidelines of the journals of submission and are at the end of each chapter. The environmental history chapter includes a footnote referencing system, whereas the second, scientific, chapter uses APA. As the chapters are written as independent papers, there may be some repetition evident among chapters. Overall, the layout of both chapters is significantly different, but both aim to contribute valuable insights in regard to marine wood borers.

References

Baratti M, Filippelli M, Messana G (2011) Complex genetic patterns in the mangrove wood-borer *Sphaeroma terebans* Bate, 1866 (Isopoda, Crustacea, Sphaeromatidae) generated by shoreline topography and rafting dispersal. Journal of Experimental Marine Biology and Ecology 398:73-82

Barnaby N (1860) On mechanical invention and its relation to the improvement of naval architecture. In: Reed EJ (ed) Transactions of the Royal Institute of Naval Architects, volume 1. The Institution, London, p 175

Blakeslee AMH, Byers JE, Lesser MP (2008) Solving cryptogenic histories using host and parasite molecular genetics: the resolution of *Littorina littorea*'s North American origin. Molecular Ecology 17:3684-3696

Borges LMS, Sivrikaya H, le Roux A, Shipway JR, Cragg SM, Costa FO (2012) Investigating the systematics of marine wood borers (Bivalvia: Teredinidae) combining evidence from morphology, DNA barcodes and nuclear locus sequences. Invertebrate Systematics 26:572-582

Borojevic K, Steiner W, Gerisch R, Zazzaro C, Ward C (2010) Pests in an ancient Egyptian harbour. Journal of Archaeological Science 37:2449-2458

CABI (2013) Invasive species compendium: Limnoria lignorum and Limnoria quadripunctata. http://www.cabi.org/isc. Accessed 12 January 2014

Carlton JT, Hodder J (1995) Biogeography and dispersal of coastal marine organisms: experimental studies on a replica of a 16th-century sailing vessel. Marine Biology 121:721-730

Carlton JT (1996) Biological invasions and cryptogenic species. Ecology 77(6):1653-1655

Chiarappa M, McKenzie M (2013) New directions in marine environmental history: an introduction. Environmental History 18:3-11

Cookson LJ (1986) Marine borers and timber piling options. Research Review CSIRO, Australia

Cookson LJ (1991) Australasian species of Limnoriidae (Crustacea: Isopoda). Memoirs of the Museum of Victoria 52:137-262

Costa PO, deWaard JR, Boutillier J, Ratnasingham RTD, Hajibabaei M, Hebert PDN (2011) Biological identifications through DNA barcodes: the case of Crustacea. Canadian Journal of Fisheries and Aquatic Science 64(2):272-295

Cragg SM (1993) Wood break-down in mangrove ecosystems: a review. Papua New Guinea Journal of Agriculture, Fisheries & Forestry 36:30-39

Davidson TM (2006) The invasion of the Australasian burrowing Isopod (*Sphaeroma quoianum*) in Coos Bay, Oregon. Master's thesis, University of Oregon

Davidson TM, de Rivera CE (2012) Per capita effects and burrow morphology of a burrowing Isopod (*Sphaeroma quoianum*) in different estuarine substrata. Journal of Crustacean Biology 32(1):25-30

Elder P (1856) The natural history of Pliny, volume 5. G. Bell & Sons, Michigan

Fofonoff PW, Ruiz GM, Steves B, Carlton JT (2003) In ships or on ships? Mechanisms of transfer and invasion for nonnative species to the coasts of North America. In: Ruiz GM, Carlton JT (eds) Invasive Species Vectors and Management Strategies. Island Press, Washington pp 152-182

Geller JB, Darling JA, Carlton JT (2010) Genetic perspectives on marine biological invasions. Annual Review of Marine Science 2:367-393

Gordon DP (2011) Marine biodiversity, Alpha 108. The Royal Society of New Zealand, Wellington

Gregory D (2010) Shipworm invading the Baltic? International Journal of Nautical Archaeology 39:431

Hayden BJ, Inglis GJ, Schiel DR (2009) Marine invasions in New Zealand: a history of complex supply-side dynamics. In: Rilov G, Crooks JA (eds) Biological Invasions in Marine Ecosystems. Springer-Verlag, Berlin Heldelberg pp 409-423

Haye PA, Varela AI, Thiel M (2012) Genetic signatures of rafting dispersal in algal-dwelling brooders *Limnoria* spp. (Isopoda) along the SE Pacific. Marine Ecology Progress Series 455:111-122

Hebert PDN, Cywinska A, Ball SL, deWaard JR (2003) Biological identifications through DNA barcodes. Proceedings of the Royal Society 270:313-321

Herbert PDN, Ratnasingham S, deWaard JR (2003b) Barcoding animal life: Cytochrome *c* oxidase subunit 1 divergences among closely related species. Proceedings of the Royal Society 270:S96-S99

Hickey JR, Lavery SD, Hannan DA, Baker SC, Clements KD (2009) New Zealand triplefin fishes (family Tripterygiidae): contrasting population structure and mtDNA within a marine species flock. Molecular Ecology 18:680-696

Holthuis LB (1949) The Isopoda and Tanaidacea of the Netherlands, including a description of a new species of *Limnoria*. Zoolofische mededelingen Rijksmuseum van Natuurlijke Historie te Leiden 30:163-190

Hurley DE, Jansen KP (1977) The marine fauna of New Zealand: Family Sphaeromatidae (Crustacea Isopoda: Flabellifera). New Zealand Oceanographic Institute, Wellington

Invasive Species Specialist Group (2008) Global Invasive Species Database. http://www.issg.org/database/species/ecology Accessed 5 June 2008

Jenkins DA (2003) Active voice? Usually best. Passive voice? Sometimes better. Writing 25:26-27

Johns PM (2010) New Zealand inventory of biodiversity: Phylum Arthropoda, Subphylum Crustacea. In: Gordon DP (ed) Volume 2 Kingdom Animalia. Canterbury University Press, Christchurch pp 99-222

Knight J (2003) Scientific literacy: clear as mud. Nature 423:376-378

Knox MA, Hogg ID, Pilditch CA (2011) The role of vicariance and dispersal on New Zealand’s estuarine biodiversity: the case of *Paracorophium*

(Crustacea: Amphipoda). Biological Journal of the Linnean Society 103:863-874

McKoy JL (1980) Distribution of shipworms (Bivalvia: Teredinidae) in the New Zealand region. New Zealand Journal of Marine & Freshwater Research 14:263-275

McQuire AJ (1964) A note on the occurrence of marine borers in New Zealand. Proceedings of the New Zealand Wood Preservers Association 4:35-44

McQuire AJ (1965) Occurrence of marine wood borers in New Zealand. New Zealand Timber Journal 12:34-39

Morison SE (1942) Admiral of the Sea. Little Brown and Company, Boston

Nicholas DD (1973) Wood deterioration and its prevention by preservative treatments. http://books.google.co.nz/books Accessed 8 August 2013

Nikula R, Fraser CI, Spencer HG, Waters JM (2010) Circumpolar dispersal by rafting in two subantarctic kelp-dwelling crustaceans. Marine Ecology Progress Series 405:221-230

Repko AF (2008) Interdisciplinary research, process and theory. Sage Publications, Inc., United States pp 3-31

Roman J, Darling JA (2007) Paradox lost: genetic diversity and the success of aquatic invasions. Trends in Ecology and Evolution 22:454-464

Ross PM, Hogg ID, Pilditch CA, Lundquist C J (2009) Phylogeography of New Zealand's coastal benthos. NZ Journal of Marine and Freshwater Research 43:1009-1027

Ross PM, Hogg ID, Pilditch CA, Lundquist CJ, Wilkins RJ (2012) Population genetic structure of the New Zealand estuarine clam *Austrovenus stutchburyi* (Bivalvia: Veneridae) reveals population subdivision and partial congruence with biogeographic boundaries. Estuaries and Coasts 35:143-154

Ruiz GM, Carlton TJ (2003) Invasive species, vectors and management strategies. Island Press, Washington p ix

San Francisco Bay Marine Piling Committee (1927) Final report of the San Francisco Bay Marine Piling Committee, historical section. In: Hill CL and Kofoid CA (eds) Marine Borers and their relation to marine construction on the Pacific Coast. University of California Press, California pp 1-3

Santhakumaran LN (2003) Wood-borers. UNU-INWEH Course 1-International Training Course on Mangroves and Biodiversity. Centre of Advanced Studies in Marine Biology, Annamalai University, India, pp 425-437

Santos SML, Tagliaro CH, Beasley CR, Schneider H, Sampaio I, Filho CS, de Paula Muller AC (2005) Taxonomic implications of molecular studies on Northern Brazilian Teredinidae (Mollusca: Bivalvia) specimens. Genetics and Molecular Biology 28:175-179

Simberloff D, Brown BJ, Lowrie S (1978) Isopod and insect root borers may benefit Florida mangroves. Science 18:630-632

Sket B, Bruce NL (2004) Sphaeromatids (Isopoda, Sphaeromatidae) from New Zealand fresh and hypogean waters, with description of *Bilistra* n. gen. and three new species. Crustaceana 17:1347-1370

Stevens MI, Hogg ID, Chapman MA (2002) The corophiid amphipods of Tauranga Harbour, New Zealand: evidence of an Australian crustacean invader. Hydrobiologia 474:147–154

Svarvarsson J, Osore MKW, Ólafsson E (2002) Does the wood-borer *Sphaeroma terebans* (Crustacea) shape the distribution of the mangrove *Rhizophora mucronata*? Ambio 31:574-579

Thunberg CP (1796) Travels in Europe, Africa and Asia, performed between 1770-1779. Oxford University, Oxford p 127

Turner RD (1966) A survey and illustrated catalogue of the Teredinidae. Museum of Comparative Zoology Harvard University, Cambridge

Chapter II

Boring through history: An environmental history of marine wood borers' extent, impact and management in a global and New Zealand context

*To be published under the same title as: Rayes C, Beattie J, Duggan I

Abstract

This paper seeks to address the lack of understanding of the historic global impacts and responses to marine wood borers, with particular reference to New Zealand between 1850 and 1930. Marine borers have had a profound impact throughout history, wreaking structural and economic havoc around the globe. Principally recognised for turning sturdy seaworthy wooden ships and marine infrastructure into honeycombed wrecks, wood preservation to resist borers was, and remains, of concern to port authorities. Even with the later development and use of iron steam-ships, especially after the 1860s, wooden vessels remained important as a form of transportation just as wooden marine infrastructure, principally in the form of jetties, wharves and bridges, played a crucial role in supporting world trade. Historical evidence from New Zealand illustrates the extent of borer destruction, particularly in the period after 1850, which witnessed a significant growth in international shipping volumes. Reports of damage and management attempts increased in the decades leading up to the twentieth century, with most reported damage emerging on New Zealand's east coast, where its main international ports were located. International and local scientific research into preservation techniques and resistant timbers, as well as the trialling of woods, informed New Zealand management attempts. Repeated failure using the same techniques occurred over several decades until the more widespread and successful use of ferro-concrete pilings from the 1900s. This lengthy failure to learn from the past, and a lack of co-ordinated research into management techniques, suggests the fragmentation of colonial knowledge, as international ideas were introduced at a local-level rather than nationally.

Introduction

Marine environmental history is a largely unexplored, but dynamic and expanding area of study.[1] For example, in *Environment and History* few articles specifically address marine environmental history, despite oceans covering 71 per cent of the Earth's surface.[2] This article presents new perspectives on marine environmental history, through an examination of the arrival, spread, impact and human responses to marine wood borers—the 'Termites of the Sea'. It broadly details the global occurrences of marine woodborers, and overviews their historical spread and human responses to them. It then provides a detailed case-study of marine wood borers in New Zealand, tracing past problems and management attempts from the arrival of the first humans, in *c.*1300, to the 1930s, by which time their impacts were lessening. Given the lack of attention paid to the history of these organisms, the initial aim of the article is to provide greater understanding of their destructive effects, and to acknowledge marine wood borers as playing a significant role in world environmental history, through their impact on wooden structures and in human attempts to mitigate their effects.

Wooden vessels and marine infrastructure have played a crucial role in supporting world trade and economics, particularly in the period after the 1860s, and have subsequently provided the habitat for borers to thrive in. Extensive borer damage is prevalent throughout New Zealand's history, with increasing reports of destruction between 1850 and the twentieth century, a period which witnessed a significant growth in shipping, migration and global interactions. The majority of early reported damage emerged on New Zealand's east coast, where its main

---

[1] Michael Chiarappa and Mathew McKenzie, 'New Directions in Marine Environmental History: An Introduction', *Environmental History* 18 (2013): 3—11.

[2] Aldemaro Romero et al., 'Environmental History of Marine Mammal Exploitation in Trinidad and Tobago, W.I., and its Ecological Impact', *Environment and History* 8 (2002): 255—274; Jonathan Clapperton, 'Desolate Viewscapes: Sliammon First Nation, Desolation Sound Marine Park and Environmental Narratives', *Environment and History* 18 (2012): 529—559.

international ports were located. International and local scientific research into preservation techniques and resistant timbers formed the foundation of New Zealand's management attempts. Prior to the more widespread use of ferro-concrete pilings from the 1900s, New Zealand's management attempts consisted of repeated trial and error of the same techniques over several decades. This historical evidence from New Zealand highlights the significant extent of marine wood borer impacts and the lengthy failure to learn from past management attempts.

Historiography

Timber has played a fundamental role in human society. For millennia, it has provided the main construction material for wooden ships and marine infrastructure—both of which have presented an appetizing opportunity for marine wood borers. Shipworms, pillbugs and gribbles are the three groups of marine wood borers that have wreaked havoc on such structures, by turning sturdy and seaworthy wooden ships into honeycombed wrecks. They have also rapidly eaten away at marine infrastructure throughout the world—wharves, jetties, bridges and other structures have all fallen prey to their depredations.

As a result, marine wood borers have had an important, if largely unacknowledged, impact on the social, economic and political history of the world, particularly in the period after 1800, which witnessed a massive growth in shipping networks based on increasing migration and volumes of trade.[3] Most of this movement largely relied, until the 1860s, on wooden ships, and their associated timber infrastructure. Even after this decade, wooden vessels remained an important mode of transportation. In this respect, marine wood borers created

[3]Patrick Manning, *Migration in World History* (New York: Routledge, 2005), pp.132-156; C.A. Bayly, *The Birth of the Modern World, 1780-1914* (Malden, Mass.: Blackwell Publishing, 2004).

headaches for governments, shipping companies and export industries, as authorities and companies grappled with the problems of crumbling infrastructure and ships. A variety of solutions spurred the exchange of new timber resources and the commissioning of engineering and scientific studies into woods able to resist the borer, as well as research into treatments of woods and alternative building materials. However, the problem persists: although borer devastation lessened following the use of alternative building materials and preservatives, a global estimate in the early 2000s stated that borers still cause US$1 billion worth of damage per year.[4]

Despite the widespread historical persistence and importance of marine wood borer damage, little scholarship outside of science has examined its extent, impact, or the societal responses to it. To date, environmental historians have largely neglected marine wood borers, relegating them largely to a footnote in wider studies.[5] Such neglect perhaps reflects marine environmental history's primary focus, on the depletion of fisheries. Nonetheless, we argue that marine wood borers played a significant role in world environmental history, and have a lasting presence as 'one of the most serious marine pests in the world … over the last few hundred years'.[6]

Highlighting the role of wood borers in history adds significant new perspectives to marine environmental history, especially to understandings of the wooden world of our past, a time when both the construction of wooden maritime structures was commonplace and when wooden vessels conveyed much of the

---

[4] Kristin Cobb, 'Return of a Castaway', *Science News* 162 (2002): 72—74.
[5] With the exception of a few isolated mentions, see: J. R. McNeill, 'Woods and Warfare in World History', *Environmental History* 9 (2004): 398; John Waldman, *Heartbeats in the Muck: The History, Sea Life, and Environment of New York Harbor*, Revised Edition (USA: Fordham University Press, 2013), pp.61-2.
[6] Kunio Tsunoda, 'Ecological Studies of Shipworm Attack on Wood in the Sea Water Log Storage Site', *Wood Research Institute Kyoto University* 65 (1979): 11—53.

world's trade, and significant numbers of the world's people. Aside from its contribution to marine environmental history, essential knowledge of the why, how, when and where of marine wood borers can help provide a foundation for scientific understanding and current vector management.[7] More specifically, New Zealand records of marine borer issues and management attempts provide a detailed background to neglected social, cultural and economic aspects of imperial expansion, which itself, through global demands for natural resources, re-shaped the movement of wood borers around the globe. This focus is particularly pressing given the relative neglect of marine systems in New Zealand's environmental history.[8] While there are innumerable studies of the introduction of terrestrial plants, animals and organisms in connection with New Zealand's colonisation,[9] none has examined marine resources in environmental history. In examining shipworm impacts on marine infrastructure, this article also considers the connections between marine and terrestrial environmental history; between histories of sea and histories of the land.

---

[7] Gregory M. Ruiz and James T. Carlton, *Invasive Species, Vectors and Management Strategies* (Washington: Island Press, 2003).

[8] Eric Pawson and Tom Brooking, 'Epilogue', in Pawson and Brooking (eds.), *Making a New Land: Environmental Histories of New Zealand*, new edition pp.328-335 (Dunedin: Otago University Press, forthcoming); James Beattie, 'Recent Directions in the Environmental Historiography of the British Empire', *History Compass*, 10, 2 (2012): 129—139; Beattie, 'Greener Pastures? Future Research Topics on New Zealand's Environment', *ENNZ: Environment and Nature in New Zealand*, 1, 2 (2006): 8—13.

[9] Alfred W. Crosby, *Ecological Imperialism: the biological expansion of Europe, 900-1900* (Cambridge: Cambridge University Press, 1986); Thomas Dunlap, *Nature and the English Diaspora: Environment and History in the United States, Canada, Australia, and New Zealand* (Cambridge: Cambridge University Press, 1999); McGlone, Matt, 'The Polynesian Settlement of New Zealand in Relation to Environmental and Biotic Changes', *New Zealand Journal of Ecology* 12 (1989): 115—129; Beattie, 'Biological Invasion and Narratives of Environmental History in New Zealand, 1800-2000', in Ian D. Rotherham and Robert A. Lambert, (eds.), *Invasive and Introduced Plants and Animals: Human Perceptions, Attitudes and Approaches to the Environment*, pp.343-352 (London; Washington, D.C.: Earthscan, 2011); King, Carolyn, *Immigrant Killers* (Auckland: Oxford University Press, 1984); R.C. Lamb, *Birds, Beasts & Fishes: The First Hundred Years of the North Canterbury Acclimatisation Society* (Christchurch: North Canterbury Acclimatisation Society, 1964); Paul Star, 'New Zealand's Biota Barons: Ecological Transformation in Colonial New Zealand', *ENNZ: Environment and Nature in New Zealand* 6 (2011): 1—12.

Origins and distributions

The complex modern distribution of many marine wood borer species, combined with the historic nature of their dispersal, makes it difficult to determine precisely their geographical origins. Their wide and varied modern distributions owe almost as much to myriad human transportation vectors—including boat hulls and ballasts—as they do to natural spread by driftwood on oceanic currents. New settlements also depended on the availability of a wood supply.[10]

Tropical coastal water bodies host the greatest diversity of marine wood borers, indicating the tropics as the likely centre of evolution and diversification of these animals, an interpretation consistent with the natural distribution of a wood supply from mangrove forests. As such, most wood-boring species prefer warmer temperatures. Whilst most commonly acknowledged for their adverse impacts, borers provide important ecological services within mangroves and along coastlines, increasing rates of decomposition and nutrient cycling, and removing the build-up of woody debris. This gives reason for the recognition of marine wood borers as an environmental wonder by some, but because of their destructive capabilities, an economic nightmare by most.

The combined damage of taxonomically distinct woodborer groups—in particular gribbles and shipworms—long made it difficult to separate their culpability. In recent years, taxonomic improvements and the identification of distinctive destruction patterns has made differentiation relatively straightforward. Shipworms are molluscan bivalves—close relatives of mussels and clams, in the family Teredinidae. Although they superficially resemble worms, they also

[10] Charles H. Edmondson, 'Teredinidae, Ocean Travellers', *Bernice P. Bishop Museum* 23 (1962): 45—59.

possess a shelled clam-like front, which assists in their drilling of wood.[11] These species enter the wood as larvae and are capable of reaching lengths of up to 100 cm, forming deep tunnels running roughly parallel to the grain—tunnels undetectable from the surface. In short, they 'wreck timber much as osteoporosis wrecks bone'.[12] Shipworm species are capable of tolerating a range of salinities, from brackish water and open seas.[13] Temperatures of between 15 and 25 degrees Celsius facilitate shipworm growth and reproduction. Some are capable of surviving temperatures below five degrees Celsius, although the contemporary distributions of most shipworms are restricted to tropical and temperate latitudes.[14] Evasion of shipworms therefore occurs only in the coldest of seas.

The crustacean isopods—Pillbugs and Gribbles—are related to the woodlouse, and belong to the families Sphaeromatidae and Limnoriidae, respectively. Gribbles are the smallest of the borers (1-4 mm) and leave visible entrances to superficial tunnels.[15] Gribbles are the least tolerant to low salinities, and more typically occur in open harbours than brackish estuaries. In contrast, Pillbugs are significantly larger crustaceans (8-14 mm), commonly found in brackish mangrove ecosystems. Unlike shipworms and gribbles that ingest wood as a food source, Pillbugs eject wooden fragments, undigested, as they bore; burrows are primarily utilised as a form of shelter.[16] Although their distinctive damage

---

[11] Robert C. Miller, 'The Boring Habits of the Shipworm', *Scientific Monthly* 19 (1924): 433—440.
[12] Cobb, 'Return', 72—74.
[13] John. L. McKoy, 'Distribution of Shipworms (Bivalvia: Teredinidae) in the New Zealand Region', *New Zealand Journal of Marine and Freshwater Research* 14 (1980): 263—273; M. Saraswathy, N. Balakrishnan Nair, 'The Influence of Salinity on a Tropical Estuarine Shipworm *Nausitora hedleyi* Schepman (Bivalvia – Teredinidae)', *Hydrobiologia* 44 (1974): 387—411.
[14] Peter Paalvast and Gerard Van Der Wald, 'New Threats of an Old Enemy: the Distribution of the Shipworm *Teredo navalis* L. (Bivalvia: Teredinidae) related to Climate Change in the Port of Rotterdam Area, the Netherlands', *Marine Pollution Bulletin* 62 (2011): 1822—1829.
[15] Lauren and Jan Cookson, *Marine Borers and Timber Piling Options* (Victoria: CSIRO, 1986).
[16] Cookson, *Marine Borers,* 1—13; Aung Si. O. Bellwood, G. C. Alexander, 'Evidence for Filter-Feeding by the Wood-Boring Isopod, *Sphaeroma terebrans* (Crustacea: Peracarida)', *Journal of Zoology* 256 (2002): 463—471.

resembles that of the gribbles, with shallow visible burrows, they prefer much lower salinities. Historically, evidence of damage to marine infrastructure and ships by pillbugs is negligible, relative to other borer families. Nevertheless, in brackish ecosystems, they are capable of causing significant harm to live mangroves, and marine infrastructure.

Overview of global impacts, science and management

Fossil records from the Cretaceous period (145-66 MYA) preserve the earliest known global presence of shipworms.[17] Although clearly present for millions of years, the adverse effects of marine wood borers were not of concern to humans until the introduction of wooden vessels and the use of marine infrastructure. Recent discoveries have dated borer damage to the second millennium BCE, through excavated hull planks found in Egypt.[18] Ma'agan Mikhael, a merchantman discovered buried 1.5 meters under sand off the Israel coast and dated to 400 BCE, had shipworm damage on its uppermost timbers.[19] The limited extent of shipworm damage on the uppermost timbers suggests borer attack occurred in the timeframe between the vessel sinking and becoming buried under the sand, and that burial likely took place soon after its submergence.

Artistic depictions of seagoing vessels in Egypt, including paintings and drawings on the walls of temples and tombs, and decorated pottery dating back to 2494-2435 BCE, provide comparable evidence that seagoing vessel designs accommodated for the destruction of borers. Vessel designs, and vessel excavations, include the use of thicker planking on seagoing vessels compared to riverine vessels, and the addition of at least five centimetres of sacrificial material

---

[17] Cobb, 'Return', 72—74.
[18] Ksenija Borojevic, Warren Steiner, Rainer Gerisch, Chiara Zazzaro, Cheryl Ward, 'Pests in an Ancient Egyptian Harbour', *Journal of Archaeological Science* 37 (10): 2449—2458.
[19] Yaacov Kahanov, 'Wood Conservation of the Ma'agan Mikhael Shipwreck', *The International Journal of Nautical Archaeology* 26 (1997): 316—329.

between joints and on outer planks, utilized to slow the borer ravages. A final step in Egypt involved applying a thin coating of pine tar on vessels to protect them against seawater and the elements, including presumably from borer damage.[20] Furthermore, Egyptian seafarers, visitors to Egypt, as well as the Phoenicians, sought high quality timber for vessel construction, favouring those of fine grain and few knots, such as Cedar (*Cedrus libani*) and Nile acacia (*Acacia nilotica*).[21] Despite such measures, ship remains provide evidence of continued borer infestation.[22]

Other early records come from Roman philosophers, poets and naturalists, who described the effects of marine bores as early as 412 BCE and chronicled the utilization of chemicals, wax and resins to preserve wooden vessels, as well as the continued use of conifer tar. Pliny the Elder described a more complex alternative to tar, known as 'zopissa', a combination of beeswax and resin. These vessel coatings sealed the timber surface, shielding the timber from the elements, and potentially minimised hull fouling and borer activity. [23]

From 500 BCE trade rapidly increased along the Mediterranean. The Greeks built larger vessels; from 300 BCE, Greek and Roman seafarers attached lead casing to their vessels using copper nails, in an attempt to resist the effects of wood borers.[24] However, copper corrosiveness became apparent after initial trials by the

---

[20] Mark E. Polzer, 'Early Shipbuilding in the Eastern Mediterranean', in A. Catsambis, B. Ford and D. L. Hamilton (eds.), *The Oxford Handbook of Maritime Archaeology*, pp. 349-378 (New York: Oxford University Press, Inc., 2011).
[21] Cheryl Ward and Chiara Zazzaro, 'Evidence for Pharaonic Seagoing Ships at Mersa/Wadi Gawasis, Egypt', *The International Journal of Nautical Archaeology* 39 (2009): 27—43.
[22] Ward and Zazzaro, 'Evidence', 27—43; McNeill, 'Woods and Warfare', 388—410.
[23] Jacques Connan and Arie Nissenbaum, 'Conifer Tar on the Keel and Hull Planking of the Ma'agan Mikhael Ship (Israel, 5th Century BC): Identification and Comparison with Natural Products and Artefacts Employed in Boat Construction', *Journal of Archaeological Science* 30 (2003): 709—719; Pliny the Elder, *The Natural History of Pliny, Volume 5* (Michigin: G. Bell & Sons, 1856), p. 19.
[24] Felipe Fernández-Armesto, *The World: A History* (Virginia: Pearson Prentice Hall, 2007).

Greeks and Romans.[25] Between 500 and 100 BCE, predictable monsoon winds facilitated increased traffic along the Indian Ocean trade routes. Aside from winter, predictable south- and west-winds blew, allowing return trips across great distances. The absence of sophisticated navigation technology, including nautical charts and compasses, meant that the fixed wind patterns of the Atlantic and Pacific oceans posed challenges to sailors, so that the utilization of Atlantic transoceanic routes did not occur until the fifteenth century.[26] At the same time, European and African sailors entered the Indian Ocean, and Europeans began to regularly journey to Africa's south-western coast.[27] New and improved preservation methods, using lead, tallow and pitch, resulted from this transoceanic voyaging of the fifteenth century. A description of a Venetian vessel outlines how 'the whole galley within and without, is covered with the blackest pitch, may not easily be rotted'.[28] Coating vessels in tallow and pitch, followed by careening and re-pitching every few months, was also performed on Columbus' entire fleet—*Santa María*, *Pinta* and *Niña*—during his first voyage in 1492.[29]

Improved maritime technology and expanding international trade in the sixteenth century opened routes between Europe, Africa and the Americas. A Pacific connection between Asia and the New World also commenced, following the European discovery of the Gulf Stream.[30] Accounts of wooden-vessel destruction and borer-resistant methods appeared more frequently in this period, coincident

---

[25] Woods Hole Oceanographic Institute (WHOI), *Marine Fouling and its Prevention* (California: United States Naval Institute, 1952), pp. 211—223. Lead sheathing reappeared on Spanish and English vessels in the fifteenth and sixteenth centuries CE, and whilst initially regarded as good marine borer resistance, corrosion later became an issue.
[26] Kenneth McPherson, *The Indian Ocean: A History of People and Sea* (Delhi: Oxford University Press, 1998).
[27] Fernández-Armesto, *The World*, 480—427.
[28] Frederick Chapin Lane, *Venetian Ships and Shipbuilders of the Renaissance* (Italy: JHU Press, 1992), p. 21.
[29] Samuel Eliot Morison, *Admiral of the Sea* (Boston: Little, Brown and Company, 1942).
[30] Fernández-Armesto, *The World*, 534—535.

with increased trade. On Columbus' fourth voyage in 1503, the 'worm-eaten' hulls of vessels *Capitana* and *Santiago* forced them to beach.[31] Despite the apparent knowledge of potential shipworm damage from earlier voyages, the lack of careening and re-pitching on this voyage meant severe damage was expected, and illustrates the extent to which shipworms impacted on oceanic voyaging.

Other nations' nations also attempted to address the problem of wood borers. In 1515, the English Royal Navy introduced wood sheathing—an additional outer layer of timber—, a method later improved by the inclusion of an under-layer of animal hair and tar.[32] Most famously, perhaps, wood borers are said to have contributed to the defeat of the Spanish Armada, whose vessels suffered from severe deterioration when sailing to Britain in 1588.[33] Marine wood borers continued to challenge the expanding horizons of trade and exploration, making the discovery of a more effective method against woodborers ever more urgent.

In the mid-eighteenth century, the Japanese employed a method of scorching their vessels in charcoal.[34] Around the same time, Royal Naval architects utilized lead fastenings, copper nails, and brimstone (sulphur)—methods suggesting the failure of earlier wooden-sheathing attempts.[35] Yet these, and other methods, also failed. Perhaps the most famous early-modern case of marine borer impact on land involved *Teredo navalis*. This devastated Netherland's wooden seawalls in 1731, only one year after its first recorded appearance. Attempts to repair the damage cost hundreds of thousands of Guilders, with arsenic, iron coatings, plates and

---

[31] Cobb, 'Return', 72—74; Morison, *Admiral of the Sea*, 633—634.
[32] Nathaniel Barnaby, 'On Mechanical Invention in its Relation to the Improvement of Naval Architecture', in E. J. Reed (ed.), *Transactions of the Royal Institute of Naval Architects, Volume 1,* p. 145 (London: The Institution, 1860).
[33] Barry Goodell, Darrel Nicholas, Tor Scholtz, *Introduction to Wood Deterioration and Preservation* (Mississippi: Mississippi State University, 2003), p. 167.
[34] Charles Peter Thunberg, *Travels in Europe, Africa, and Asia Performed Between 1770-1779* (Oxford: Oxford University, 1796), p. 127.
[35] Barnaby, 'On Mechanical Invention', p. 151.

nails, and eventually stones employed to protect the dikes from borers.[36] Despite such attempts, *T. navalis* caused further destruction to other submerged structures along Netherland's coast well into nineteenth century.[37] The extensive damage and economic impact of shipworms motivated scientific exploration into their anatomy in the eighteenth century.[38]

While trading voyages subjected vessels to the depredations of shipworms, it also offered them opportunities of finding borer-resistant timbers. Cuban cedar (*Cedrela odorata*) and the Cabopa tree (*Mitragyna stipulosa*) from Cacheu, Africa, seemed to provide shipworm resistance.[39] The Spanish Navy built around one-third of their vessels in Cuba during the eighteenth century, demonstrating clearly a connection between perceived shipworm resistant timbers and the location of naval dockyards.[40] Although thought to 'last well' in shipworm infested waters, longer term resistant methods replaced these trees by the late eighteenth century. The first long-term preservation success against wood borer arose in the eighteenth century using copper sheathing. Based on their success with this method on the naval vessel, *Alarm*, whose thin copper plating gave it 10 years' resistance to wood borer, from 1777, the Royal Navy started to place a thin copper layer over all of its vessels. Late in that century, the United States Navy followed suit. Yet even with copper plating, general wear caused sheathing to detach from hulls, exposing timber to borers. Sheathing also required periodic removal of the oxidised copper surface after it reacted with the seawater. Moreover, the unpredictable nature of copper's antifouling properties and its

---

[36] Paalvast, Velde, 'New Threats of an Old Enemy', 1822—1829; *Daily Southern Cross (DSC),* 29 Jan. 1869, 2.
[37] Paalvast, Velde, 'New Threats', 1822—1829.
[38] Ruth D. Turner, *A Survey and Illustrated Catalogue of the Teredinidae* (Cambridge: Museum of Comparative Zoology, 1966).
[39] Saheed Aderinto, 'Shipyards', in T. Falola and A. Warnock (eds.) *Encyclopedia of the Middle Passage*, pp. 343-344 (Texas: Greenwood Publishing Group, 2007).
[40] McNeill, 'Woods and Warfare', 388—410.

constant rate of wear, made it difficult to determine the success of any one copper-sheathed vessel.[41] Copper sheathing—initially regarded as an infallible woodborer defence—thus became an inadequate long-term solution.

Although nineteenth-century European industrialization resulted in a gradual increase in the use of iron vessels, timber continued to be utilized as a cheaper, more resilient option, perhaps because of a persistent belief that an effective long-term preservation method would be found.[42] The navies of Britain and the USA even chose to sheath some of their new iron vessels with wood, followed by a copper layer, to prevent fouling and corrosion of the iron hull, although the high costs restricted the use of such extensive preservation methods, and antifouling paints of metallic composition became a commonly-used alternative later in the nineteenth century.[43] Regardless of the multitude of trialled compositions—including copper, mercury, arsenic, turpentine and resins—marine-borer continued to challenge oceanic travel**.**

Problems of borer damage also affected newly developing communications technology. Engineers indicted *Teredo* species as one of the 'principle sources of injury' to nineteenth-century submarine telecommunication cables, because they ate right through protective outer layers into the cable core.[44] For example, in 1859 scientists identified the problems affecting a submarine cable laid between Canada and Egypt as the 'enemy' shipworm—a common description of such organisms.[45] The potential for marine wood borers to penetrate toxic vessel paints, sheathing and cable insulation continued to disrupt communications throughout the nineteenth century.

---

[41] WHOI, *Marine Fouling and its Prevention,* 211—223.
[42] Cookson, *Marine Borers,* 1—14.
[43] WHOI, *Marine Fouling and its Prevention,* 211—223.
[44] James Anderson, 'Ocean Cables', *The Popular Science Monthly* 3 (1873): 42—44.
[45] Anderson, 'Ocean Cables', 42—44.

The widespread and varied damage of wood borers in such an age of increased communications renewed scientific interest in borer taxonomy and systematics, allowing for better differentiation among genera and species. Nineteenth-century research included work by British zoologists: John Edward Gray (shipworms), William Elford Leach (British molluscs), and Sylvanus Charles Thorp Hanley and naturalist Edward Forbes (six 'endemic' British shipworms). Significant destruction in the nearby Dockyard at Plymouth, England, prompted such interests.[46] In the 1860s, scientific research expanded, with a survey of shipworms in the United States undertaken by malacologist George Washington Tyron, and the analysis of material sent from India and Australia by Edward Percival Wright, professor of zoology at the University of Dublin.[47] Whilst pillbugs and gribbles also received taxonomic attention, shipworms appeared to be the most studied group in that century, possibly because their comparatively large size drew them more attention, and thus made identification and discovery easier.

Early in the twentieth century, one of the most well cited instances of borer damage occurred in San Francisco Bay, California. *T. navalis* severely damaged infrastructure in northern San Francisco Bay, including causing the collapse of several structures in the Carquinez Strait (Fig 1).[48] With damage described as 'astronomical', the estimated economic cost inflicted by shipworms in San Francisco Bay over only a two year period from 1919 was US$500 to 900 million dollars (based on 2009 dollar values).[49] Following the transition of timber to iron

---

[46] Turner, *A Survey and Illustrated Catalogue*, 10—13.
[47]Charles Chilton, 'Further Additions to our Knowledge of New Zealand Crustacea' *Transactions and Proceedings of the Royal Society of New Zealand* (1882): 1—24; Turner, *A Survey and Illustrated Catalogue*, 10—13.
[48] C. L. Hill, C. A. Kofoid, *Marine Borers and their Relation to Marine Construction on the Pacific Coast* (San Francisco: San Francisco Bay Marine Piling Committee California, 1927), 1—4.
[49] Michael L. Elam, 'Pacific Northwest Invasive Species Profile: Great Naval Shipworm *Teredo navalis*' (Washington: University of Washington, 2009), 1—10. Actual costs of shipworm damage likely exceeded the estimated amount.

and steel-hulled vessels, borers also attacked abandoned wooden ships in the Bay.[50] The significant destruction initiated the formation of the San Francisco Bay Marine Piling Committee, to undertake local studies of borer activity. As an indication of on-going borer problems, several other groups were founded from 1920 to undertake marine-borer research, including a group developed by William F. Clapp, run by the United States' National Research Council and supported by the United States Navy, and the 22nd Special Committee, directed by the Japanese Association for Academic Advancement.[51] Clearly, then, wood borers had become an internationally significant problem by the early decades of the twentieth century, one leading to international scientific collaboration.

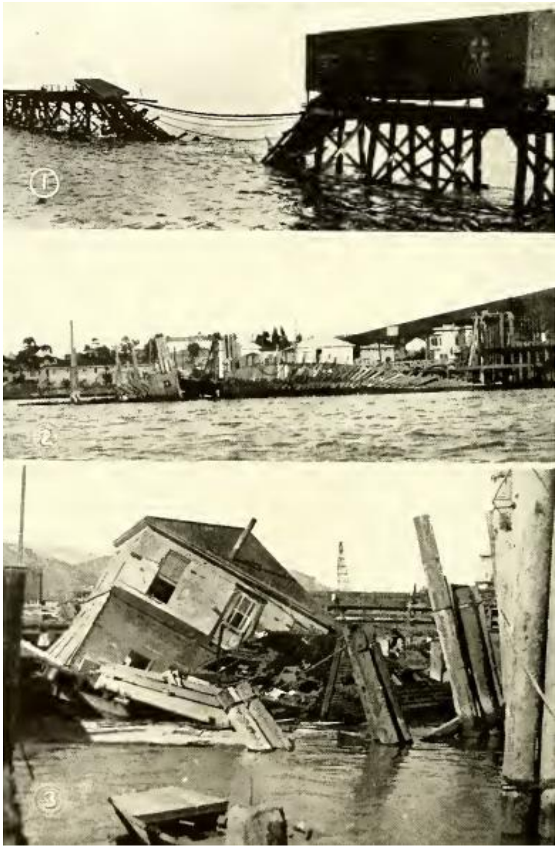

Figure 1 Dock failure (1919), Ferry slip (1920) and wharf and house collapse (1920), resulting from marine woodborer damage in the Carquinez Strait, which drains into northern San Francisco Bay, California. Source: U.S. Geological Survey, Department of the Interior/USGS: http://sfbay.wr.usgs.gov/benthic_eco/exotic_species/what_shipworm.html.

[50] George D. Buckley, Lecture in ENVR E-110 (Ocean Environments), Harvard Extension School, 20 February 2011.
[51] Tsunoda, 'Ecological Studies of Shipworm Attack', 11—53.

By this time, the decline in use of timber vessels meant that wood borers' impact receded into distant memory among seafarers. Nevertheless, the impacts of wood borers on coastal infrastructure, timber, and mangroves, continued unabated, prompting extensive research in response to its on-going economic impacts. For example, between 1995 and 1997, New York experienced severe borer damage, resulting in a 21-metre wharf section dropping into the East River and a 6-metre section plunging from the Brooklyn pier.[52] This unforeseen destruction continued into the year 2000, when the dreaded shipworm invaded Maine's docks and pilings.[53] These examples represent only a fraction of the structural and economical damage marine wood borers have caused in the United States, let alone worldwide.

Furthermore, along Florida's south-western coast, pillbug consumption is responsible for shrinking the area of mangrove forests.[54] This is by no means an isolated case. An extensive survey of marine-borers along India's Goa coast revealed severe borer damage on mangroves.[55] Both situations draw attention to the additional adverse role borers play in natural mangrove ecosystems.

New Zealand perspectives, 1850-1930

The detailed case-study of New Zealand which follows provides the most thorough discussion yet, of the impact of wood borers in environmental history. It also provides a hitherto overlooked aspect of the spread of global commerce associated with colonisation and the introduction of new species. As such, it

---

[52] Lisa Foderaro, 'Cleaner Harbor has a Downside: Pests that Plague Park Construction', *The New York Times,* 23 Aug. 2011.
[53] Cobb, 'Return', 72—74.
[54] Andrew Rehm and Harold J. Humm, '*Sphaeroma terebrans*: a Threat to the Mangroves of Southwestern Florida', *Science* 182 (1973): 173—174.
[55] L. N. Santhakumaran, 'Incidence of Marine Wood-Borers in the Mangroves of the Vicinity of Panaji Coast, Goa', *Oceanography* 16 (1983): 299—307.

complements existing scholarship on exotic terrestrial and fresh-water species consequent with New Zealand's colonisation.[56]

The case-study of New Zealand was chosen for several reasons. First, the online 'Papers Past' database provides fully key-word searchable access to colonial newspapers covering 1839 to 1945, making available over three million articles, from 83 newspapers, across the whole of New Zealand. For this study, this enabled the identification of approximately 2000 articles on borer damage over a period from 1840 to the 1930s. Second, following its colonisation in 1840, New Zealand official statistics recorded in detail the shipping movements into and out of the country, invaluable in attempting to piece together the pattern, distribution and management of shipworms. Together, these provide invaluable—and possibly unprecedented—information about the spread, impact and management of shipworms across an entire country.

This section focuses on the impact of borers on marine infrastructure, a choice shaped by several factors. The complexity and difficulty of obtaining detailed information on shipbuilding in New Zealand and overseas, not to mention the difficulty of identifying thousands of ships visiting these shores, precluded the article's focus on the impact of shipworms on vessels. Most importantly, too, unlike the global historical focus on damage to wooden ships by wood borers, New Zealand ship damage was seldom reported. Greater vessel speeds and shorter port stop-overs, combined with increased use of preservative measures and active monitoring, as well as steel ships, decreased destruction. In contrast, stationary marine infrastructure left them more susceptible to attack and therefore more of a concern in New Zealand.

[56] See note 8.

Shipworms were present around New Zealand well before its human colonization around 1300 AD, with local fossil evidence indicating their existence from around the time the New Zealand landmass developed on the edge of Gondwana (around 200 million years ago), and again from the middle Miocene.[57] Unlike shipworms, no pillbug and gribble fossils are known. At the time of human arrival, mangrove forests in the warmer north of New Zealand, comprising of *Avicennia marina* subsp. *australasica*, provided borers with a natural habitat.[58] The arrival of humans will have provided them with further suitable habitats to exploit and expand their distribution. However, of the gribble and pillbug species known today, few are considered New Zealand natives.[59] The historic nature of marine introductions, and the fact these were incidental rather than intentional, as well as the current widespread distribution of some marine wood borers, makes it difficult to distinguish native from invaders.[60]

Early human introductions, post 1300

Introductions of non-native marine species into New Zealand probably took place with the arrival of the first peoples to the islands, with coastal exploration and exchange of resources then enabling their spread. Māori—the indigenous people of New Zealand—arrived around 1300 from the eastern Pacific, bringing with them the first non-native terrestrial species, including seeds, crops, domestic dogs

---

57 John L. McKoy, 'Records of Upper Cretaceous and Tertiary *Bankia* Gray (Mollusca: Teredinidae) from New Zealand', *New Zealand Journal of Marine and Freshwater Research* 12 (1978): 351—356.

58 Willem P. de Lange and P. J. De Lange, 'An Appraisal of Factors Controlling the Latitudinal Distribution of Mangrove (*Avicennia marina* var. *resinifera*) in New Zealand', *Journal of Coastal Research* 10 (1994): 539—548.

59 Cryptogenic status is given to a species with an unknown origin, preventing differentiation between native and non-indigenous.

60 Barbara J. Hayden, Graeme J. Inglis, David R. Schiel, 'Marine Invasions in New Zealand: a History of Complex Supply-Side Dynamics', in G. Rilov and J. A. Crooks (eds.), *Biological Invasions in Marine Ecosystems,* pp. 409-421 (Berlin: Springer-Verlag, 2009).

and *kiore* (rats), as well as a number of potentially unrecognised marine species.[61] In particular, the wooden canoes (*waka*) Māori used to reach New Zealand might have provided a vector for the first human-mediated introduction of wood borers.

As arrivals from more tropical Polynesian climates—where canoes made from the Breadfruit tree (*Artocarpus altilis*), chosen partly for its resistance to borers, were common—it is possible that early Māori were already acquainted with marine wood borers prior to their arrival in New Zealand.[62] Māori awareness of marine wood borers is also inferred by the utilization of native Tōtara (*Tōtara podocarpus*) as the primary wood of waka construction.[63] Its alleged imperviousness to borers, and Māori reference to shipworms using at least two names, *Korotipa* and *Korotupa*, signal an early understanding of borer ravages and of resistance methods.[64] Furthermore, Māori coated waka hulls in shark-fin oil, said to preserve paintwork,[65] and to deter borers.[66] This interpretation is supported by the historical use of shark fin oil on a global scale; for example, Goa fishermen similarly coat their vessels in crude fish-oil to reduce borer susceptibility.[67]

Between 1500 and 1800, Māori, responding to rising population placing pressure on resources, established villages at river mouths to optimise coastal and land

---

[61] David Young, *Our Islands, Our Selves, A History of Conservation In New Zealand* (Dunedin: University of Otago Press, 2004) , p. 43; Shane T. Ahyong, Serena L. Wilkens, 'Aliens in the Antipodes: Non-Indigenous Marine Crustaceans of New Zealand and Australia', in B. S. Galil, P. F. Clark and J. T. Carlton (eds.), *In the Wrong Place –Alien Marine Crustaceans: Distribution, Biology and Impacts*, pp. 451-483 (Netherlands: Springer, 2011).

[62] Paul D'Arcy, *The People of the Sea: Environment, Identity, and History in Oceania* (Manoa: University of Hawaii Press, 2006), p. 90.

[63] Murray A. Bathgate, 'Maori River and Ocean Going Craft in Southern New Zealand', *The Journal of the Polynesian Society* 78 (1969): 344—377.

[64] William Leonard Williams, *A Dictionary of the New Zealand Language* (London: Williams and Norgate, 1892); Williams, *William's Maori Dictionary* (London: Williams and Norgate, 1912), p. 81; A. H. Blake, 'A Great Canoe Race', in A. H. Blake (ed.), *Sixty Years in New Zealand: Stories of Peace and War*, pp. 233-236 (New York: Gordon and Gotch, 1909).

[65] Elsdon Best, *The Maori Canoe* (Wellington: Government Printer: 1976), p. 164.

[66] Stan Conrad, op cit. Northcote College, September 26, 2013.

[67] L. N. Santhakumaran et al., 'On the Efficacy of Indigenous Method Employed along Goa Coast for Protecting Fishing Craft Against Biodeterioration', *Mahasagar-Bulletin of the National Institute of Oceanography* 15 (1982): 237—242.

resources, as well as trading opportunities.[68] As they relied largely on coastal and riverine transportation, borer activity likely had significant consequences for them. Before European arrival in the late eighteenth century and the subsequent introduction of larger trading vessels, driftwood, oceanic currents, and the limited coastal movement of waka probably restricted borer distribution. Mangrove forests would have presented the only suitable stationary habitat for borers to exploit, assuming that Māori utilized few submerged wooden structures prior to the arrival of *Pākehā* (the Māori term for non-Māori).

Mana, an essential value or spiritual power, drove early Māori to trade. Following the arrival of Pākehā in larger numbers from the early nineteenth century, trading vessels—a prestigious asset seen to acquire mana—altered their socioeconomic system, revolutionising the previously limited coastal movement of waka.[69] Trading brought goods and status,[70] and also likely provided a vector for the expansion of borer distribution, which the previously limited coastal movement of waka and lack of submerged wooden structures had largely precluded.

European arrival opened the biological floodgates to a host of new organisms, wanted and unwanted. Ship-based whaling along New Zealand blossomed from the 1790s, attracting vessels from around the world—South America, the United States, India, China, and several European countries by 1791.[71] Overseas merchants also began to exploit sealing and timber resources.[72] When compared

---

[68] Young, *Our Islands*, 37—56.
[69] Murray A. Bathgate, 'Maori River and Ocean Going Craft in Southern New Zealand', *The Journal of the Polynesian Society* 78 (1969): 344—377.
[70] Hazel Petrie, 'Bitter Recollections? Thomas Chapman and Benjamin Ashwell on Māori Flourmills and Ships in the Mid-Nineteenth Century', *New Zealand Journal of History* 39 (2005): 1—21.
[71] Petrie, *Chiefs of Industry* (Auckland: Auckland University Press, 2006), pp. 56—68.
[72] Jim McAloon, 'Resource frontiers, settler capitalism and environmental change 1770-1860', in Eric Pawson and Tom Brooking Pawson (eds.), *Environmental Histories of New Zealand*, pp. 52-68 (Melbourne: Oxford University Press, 2002); Beattie, 'Plants, Animals and Environmental Transformation: New Zealand/Indian biological and landscape connections, 1830s-1890s', in

with the natural dispersal of borers on driftwood—occurring infrequently and over smaller distances—the new human arrivals, from widespread locations, potentially increased borer introduction rates, and their spread to and from New Zealand (see below). The concentration of early international trade, particularly in the northern North Island, may have had implications for the establishment of wood borers. These northern ports, with their warmer sub-tropical climate and presence of mangroves, would have provided greatest suitability for the tropical borers in New Zealand.[73]

Colonisation by Pākehā brought settlers—and introduced organisms—in ever increasing numbers. By 1840, over 2000 Pākehā were resident in New Zealand, compared to only several hundred in 1830.[74] Thanks to immigration schemes from 1861 to 1900, some 223000 (mostly European) migrants arrived. Combined with immigration, natural increase brought New Zealand's population to some 800000 Europeans and 46000 Māori by 1901. The population rose rapidly to nearly 1.5 million people (95 per cent of European origin) by 1916, thereafter reaching a plateau in the period examined in this article—reaching 1.57 million in 1936.[75]

Over the colonial period, New Zealand's population came to rely ever more heavily on regional, national and international shipping networks for the transportation of information, goods, and people. Indeed, shipping not only made sense in such a narrow landmass, with some 15000 km of coastline, but was necessary because of its rugged, often forested and inaccessible interior, which

---

Vinita Damodaran and Anna Winterbotham, (eds.), *The East India Company and the Natural World* (Basingstoke: Palgrave Macmillan, 2014).

[73] Vincent O'Malley, *The Meeting Place, Maori and Pakeha Encounters, 1642-1840* (Auckland: Auckland University Press, 2012), pp. 11—31.

[74] Michael King, *The Penguin History of New Zealand* (Auckland: Penguin Books (NZ) Ltd, 2003), pp. 168—172.

[75] Donald Denoon, Philippa Mein-Smith and Marivic Wyndham, *A History of Australia, New Zealand and the Pacific* (Wiley-Blackwell, 2000), pp. *87*-88.

precluded the rapid development of land transportation.[76] An indication of this is that over parts of the nineteenth-century, the South Island's West Coast enjoyed closer economic and cultural ties with eastern Australia than it had with the rest of New Zealand, owing to the natural barrier to land transportation provided by the Southern Alps.[77] As well as myriad local ports and coastal shipping networks, colonists established eleven overseas trading ports around the country (Fig 2). At this time, most major Māori settlements remained in coastal Auckland and Northland regions, with further settlements centred around Wairarapa, Wellington, and Hastings; only, three per cent of the population resided in the South Island (Fig 2).[78]

---

[76] James Watson, *Links: A History of Transport in New Zealand Society* (Wellington: Ministry of Transport, Te Manatu Waka, 1996).
[77] Philippa Mein-Smith, Peter Hempenstall and Shaun Goldfinch, *Remaking the Tasman world* (Christchurch: Canterbury University Press, 2008).
[78] Kenneth B. Cumberland, 'A Land Despoiled: New Zealand about 1838', *New Zealand Geographer* 6 (1950): 13—34.

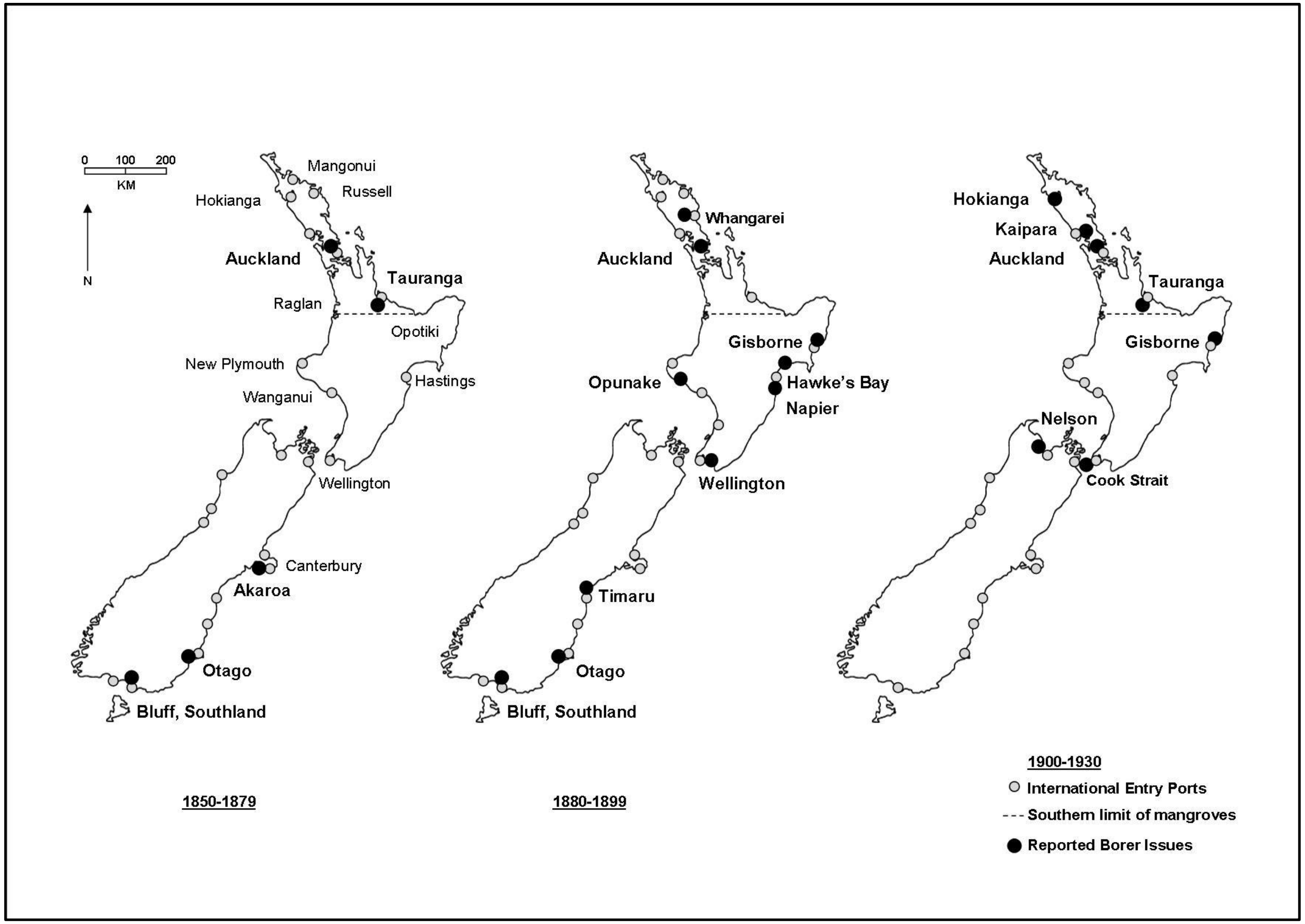

Figure 2 Reported marine borer damage around New Zealand, 1850 to 1930, displaying major trading ports — those with a value in thousands of pounds sterling (based on Peter J. Rimmer, 'The Changing Status of New Zealand Seaports, 1853-1960', Annals of the Association of American Geographers 57(1967): 91—97), and the southernmost limits of mangroves (natural marine borer habitat).

To accommodate the migrant influx brought by the development of the merino wool industry from the 1850s, and the rapid population rise following the discovery of gold in Otago in 1861, the number of overseas ports doubled between the 1850s and 1867 (Fig 2). Advances in communication and the further expansion of New Zealand's wool and timber industries also grew trade, encouraging the establishment of regular international shipping routes.[79] While trading was of utmost importance for New Zealand's economy and migration, the dumping of solid ballast and hull fouling associated with shipping, provided vectors for invasive marine species, including marine wood borers.[80] Regardless of their questionable status—native or non-indigenous—, marine-borer destruction plagued New Zealand's marine infrastructure. The following sections examine the impacts of wood borers, and the responses they generated, in New Zealand from 1850 to the 1930s, by which time wooden vessels were becoming less commonplace.

Increasing trade and borer damage, 1850-1930s

Analysis of newspaper reports reveals several key patterns in the spatial and temporal damage of wood borers in New Zealand. There is a clear increase of reported marine borer damage between 1860 and 1900, with the majority and most widespread damage occurring between 1880 and 1899 (Fig 2). This increase followed successive waves of immigration between late 1860 and the 1870s, consequent with provincial government immigration schemes, which brought greater volumes of shipping tonnage (Table 1), and a growing number of international ports and marine infrastructure, which provided opportunities for

[79] Peter J Rimmer, 'The Changing Status of New Zealand Seaports, 1853-1960', *Annals of the Association of American Geographers* 57 (1967): 88—100.
[80] Barbara J. Hayden et al., 'Marine Invasions in New Zealand: A History of Complex Supply-Side Dynamics', in G. Rilov, J. A. Crooks (eds.), *Biological Invasions in Marine Ecosystems*, p.410 (Berlin: Springer-Verlag, 2009).

borer introduction and spread, as well as suitable borer habitats. For reasons unknown, but possibly due to the greater number of port locations, increasing reports of borer damage from 1880 appeared mainly on the east coast of New Zealand, with the exception of Opunake and the far north ports (Table 1; Fig 2).

The impact of international shipping on the spread of borer is illustrated in the case-study of two ports. Whilst coastal trade took place in the harbours of Whangarei and Gisborne prior to the 1880s, the reporting of borer damage occurred only after they became international ports post-1880 (Fig 2).[81] This implies either that borers were not present prior to an increasing tonnage of international shipping (Table 1), suggesting that the ships were vectors for introduced species, or that coastal settlements failed to report any borer damage.

An overall decline in reports of damage after 1900 around New Zealand indicates success in the management of borer, notably through the use of borer-resistant ferro-concrete piles. Such improvements illustrate the importance of on-going research and experimentation, efforts which, until the gradual increase in use of ferro-concrete piles from the 1900s, largely focused on the qualities of various native and Australian timbers. In gaining knowledge about marine-borers' extent and possible preventative measures, this article stresses both the spread and limitations of colonial knowledge. Although the importance of overseas research and techniques into borer prevention demonstrate international flows of knowledge into the colony, the continued use of unsuccessful preventive measures demonstrates its limitations. In the absence of any national daily, hundreds of provincial and local newspapers catered to very local demands for knowledge, in

[81] Rimmer, 'Changing Status', 88—100.

some cases, preventing the widespread flow of knowledge around the country.[82] As historian of science David Livingstone has observed: 'Local conditions pose local problems needing local solutions.'[83]

Table 1 Reported yearly tonnage of ships cleared inwards from overseas at major New Zealand ports between 1860 and 1928. Numbers are in thousands of tonnes. Sources: The New Zealand Gazette 1870, 1880, 1890 and 1900 (Wellington: Government Printer), Statistics of New Zealand 1860 and The New Zealand Official Year Book 1920 and 1930.

Shipping Tonnage at New Zealand Ports								
	1860	**1870**	**1880**	**1890**	**1900**	**1909**	**1919**	**1928**
Mangonui	13.37	1.73	0.27	0.85	0.00	0.00	0.00	2.01
Russell	16.75	10.59	2.00	0.39	0.00	0.00	0.00	4.23
Whangarei	0.00	0.00	0.00	0.00	0.00	0.00	0.00	26.55
Auckland	36.51	72.57	125.48	184.42	315.38	554.81	684.71	1521.74
Tauranga	0.00	0.00	0.00	0.00	0.00	0.00	0.00	19.50
Gisborne	0.00	0.00	0.00	0.00	0.00	3.76	10.13	66.58
Napier	0.05	2.49	4.48	20.22	16.65	3.58	10.95	121.91
Canterbury	11.93	32.28	78.72	84.81	68.49	36.04	138.33	395.42
Timaru	0.00	0.35	5.34	19.73	20.36	8.64	4.30	51.87
Oamaru	0.00	0.84	3.10	12.87	19.36	650.00	1.22	9.23
Otago	24.72	47.52	71.35	72.40	82.86	58.57	51.53	272.87
Bluff	3.52	15.55	30.88	85.47	96.27	164.41	36.84	89.40
Wellington	11.18	21.52	63.83	151.25	203.83	399.03	519.00	1125.72
Nelson	12.36	28.99	6.77	3.48	3.30	1.57	0.47	67.96
Hokianga	2.43	0.65	0.00	0.00	0.00	0.00	0.00	13.06
Kaipara	0.36	0.70	2.54	17.18	8.01	5.31	1.36	5.20
New Plymouth	3.58	0.00	0.08	0.00	0.00	3.62	2.53	145.01
Wanganui	0.00	0.99	0.00	1.32	1.25	2.75	19.21	125.28
Westport	0.00	1.04	0.65	1.07	5902.00	15.80	0.00	18.10
Greymouth	0.00	11.37	2.28	3.96	0.85	3.26	0.32	14.75

[82] See, Beattie, *Empire and Environmental Anxiety: Health, Science, Art and Conservation in South Asia and Australasia, 1800-1920* (Basingstoke: Palgrave Macmillan, 2011); Tony Ballantyne, *Webs of Empire: Locating New Zealand's Colonial Past* (Wellington: Bridget Williams Books, 2012).
[83] David Livingstone, *Putting Science in Its Place: Geographies of Scientific Knowledge* (Chicago and London: University of Chicago Press, 2003), p. 45.

Marine Wood Borer Damage and Management Attempts, 1840s-1870s

Although the British zoologist John Edward Gray identified *Teredo* sp. in New Zealand in the 1840s,[84] in this decade and into the next, colonial newspapers mostly carried articles on overseas preservation methods rather than reports of any specific damage in the colony.[85] New Zealand literature rarely considered gribble control, despite reports of global damage.[86] Although the discussion of wood borer prevention methods suggests a demand for such articles, colonial newspapers carried no articles on their impact in New Zealand, probably because shipworm damage only becomes visible later, long after it has destroyed a wooden structure. For example, in 1896, a cutter from Bluff, Southland, appeared visibly intact, until the detached two-year-old planking revealed, "a piece of three by four inches does not weigh more than an ounce, would simply crumble to pieces in touching anything hard".[87] The earliest account of New Zealand gribble damage occurred in 1863 with the replacement of the Akaroa jetty in Lyttleton, South Island, due to borer damage sustained over the previous five years.[88]

Despite surveying all of New Zealand colonial newspapers available on-line, Lyttleton, Auckland, Otago and Southland remained the only areas of reported borer activity until the late 1870s (Map 1).[89] The discovery of gold in Otago and the expansion of Lyttleton's port in association with the region's booming wool industry, as well as Port of Auckland's position as the largest timber exporter, and importer by total value, may account for these patterns. Yet it is remarkable that

---

[84] John Edward Gray, 'Catalogue of the species of Mollusca and their shells, which have hitherto been recorded in New Zealand', cited in E. Dieffenbach (ed.), *Travels in New Zealand Volume 2*, pp. 228-265 (London: William Clowes and Sons, 1843).
[85] *DSC*, 13 Jun. 1854, 2; *New Zealander*, 22 Mar. 1851, 4
[86] *Nelson Examiner and New Zealand Chronicle (NZC)*, 2 Nov. 1850, 144.
[87] *Star*, 9 Oct. 1896, 2.
[88] *Lyttleton Times (LT)*, 15 Aug. 1863, 2. Note also, Auckland's attempts: *DSC*, 9 Nov. 1864, 5; 11 Feb. 1869, 5.
[89] *DSC*, 11 Feb. 1869, 5.

Wellington received little discussion, despite its status as a major trading port and exporter of wool from the southern North Island.[90]

As well as indicating the areas where wood borers were a problem, 1860s newspapers also carried news of major progress in the use of preservations in New Zealand. Such progress may have reflected the growing importance of shipping to the sheep trade, as New Zealand sheep numbers trebled, and wool exports increased five-fold, during this decade.[91] Of the measures attempted, impregnating timber with creosote became very popular,[92] specifically for resisting *T. navalis.*[93] The focus on measures against this species probably reflected fears about their overseas, especially their renowned destructive capabilities, tolerance to a wide range of temperature and salinity regimes, coupled with the presentation of continual opportunities to transport them. Despite this, for unknown reasons, *T. navalis* has ostensibly never been identified in New Zealand.[94] This is, perhaps, a classic case of responses generated by anxieties over the likely emergence of a pest or weed species.

The scant knowledge of the species' responsible for reported damage, both historically and recently, has led to many New Zealand reports attributing damage to *T. navalis*, including one as recently as 2005.[95] Multiple borer species consuming the same pieces of wood, combined with difficulties in morphological identification of each species, has meant even today most reports give little assistance in determining which species are responsible. The problem was magnified in the nineteenth century because, as this article shows, scientific

---

[90] John B. Bennett, 'Statistics of New Zealand for 1860' *Statistics of New Zealand* 5 (1860):1—46.
[91] Riseborough, *Shear Hard Work,* 7—10.
[92] Creosote is the mixture of chemicals created by the high temperature treatment of coal tar.
[93] *DSC,* 17 Oct. 1963, 4.
[94] McKoy, 'Distribution of Shipworms', 263—275.
[95] Most recently, the 2005 collapse of the Nuhaka Rail Bridge, Hawke's Bay, saw the 'Teredo' shipworm held responsible. *Hawke's Bay Today*, 7 May 2005, 1.

knowledge of marine borers—and ability to identify different species—was limited.

Experimentation with native tree species considered naturally resistant to shipworms nonetheless took place from the 1860s—a reflection of the early period of colonial scientific investigation focused on discovering the economic benefits of the resources of a new country. Experiments using borer-resistant timber took place in Auckland and Otago, regions of reported damage, and Timaru, which later suffered severe borer damage. In 1864, several port authorities and regional bodies started importing Australian Jarrah (*Eucalyptus marginata*) because of its perceived borer resistance.[96] By the late 1860s, Jarrah was utilised and planned for use in marine infrastructure at several New Zealand ports, including a new dry dock, funded by the Otago Provincial Council.[97] New Zealand imports of Jarrah for use in wharf, jetty and bridge construction, was met by the Western Australian Timber Company.[98] In 1864, the same year that Jarrah was first mentioned in New Zealand, Australian newspapers recognized the suitability of the indigenous New Zealand Kauri (*Agathis australis*) for ship-building.[99] It is surprising that New Zealand focused on imported timber, when Australia had already acknowledged Kauri's appropriateness for the same purpose. Perhaps historic use of Kauri in marine construction had already revealed a lack of borer resistance. Nevertheless, many New Zealand ports continued to utilise imported Jarrah.

In 1870, New Zealand newspapers carried Sydney correspondence on Jarrah's ineffectiveness against shipworms, and advised its replacement with another

---

[96] *DSC*, 16 Feb. 1866, 6; *DSC*, 29 Jan. 1869, 2; *LT*, 17 Nov. 1864, 2; *ODT*, 20 Jul. 1865, 6.
[97] *ODT*, 9 Jun. 1869, 4.
[98] *The Inquirer and Commercial News (Perth, WA: 1855-1901) (ICN)*, 16 Jun. 1869, 4.
[99] *ICN*, 7 Dec. 1864, 3.

Australian native, Turpentine wood (*Syncarpia glomulifera*).[100] Despite such advice, Jarrah was selected for the Wellington graving dock, a dry basin for maintenance and repair, in October of the same year.[101] Although Canterbury and West Coast newspapers also carried further correspondence from Adelaide on Jarrah's ineffectiveness, authorities in Lyttleton, Auckland and Otago continued to import it for jetty construction.[102] The continued use of Jarrah, despite its reported limitations in several regional New Zealand newspapers, may have reflected the fragmented nature of colonial knowledge transfer and the localised readership of newspapers—no daily has ever existed in New Zealand.

In 1874, the discovery of borer-resistant oil excreted by the New Zealand native Tōtara (*Podocarpus totara*), provided another local solution, one already known to Māori, as noted.[103] Aiming to determine the most suitable timber, the Auckland Harbour Board Engineer led a comparative investigation of Australian and New Zealand woods.[104] Part of this included the use of Turpentine and Jarrah sections from Mangere Bridge and Queen Street wharf, which revealed severe borer attack. Australian Ironbark (comprising various *Eucalyptus* species) was also trialled unsuccessfully. [105] The Auckland Harbour Board concluded Tōtara to be superior to Jarrah, based on the intact eleven-year-old Tōtara piles from Onehunga wharf.[106] In response, *The Western Australian* implied that Jarrah remained effective in Australia. Taking a swipe at New Zealand, it blamed Australian timbers' inability to withstand borer attack on 'a venomous patriotic insect in New

---

[100] *DSC,* 26 Jul. 1870, 4.
[101] *Wellington Independent (WI),* 13 Oct. 1870, 3.
[102] *West Coast Times,* 14 Jul. 1871, 2; *Press,* 26 Mar. 1873, 3; *Auckland Star,* 5 Oct. 1876, 2; *ODT,* 6 Apr. 1871, 2.
[103] *WI,* 29 Jan. 1874, 3.
[104] *Grey River Argus (GRA),* 20 May 1876, 3.
[105] *GRA,* 20 May 1876, 3.
[106] *New Zealand Herald (NZH),* 6 April 1876, 3.

Zealand'—Toredo, an allegation that was repeated in the next decade (see below).[107]

During the 1880s, further borer damage appeared, including Karawa bridge, Poverty Bay, requiring full replacement.[108] By 1889, the Timaru wharf had worsened even further, with the gribble damage compared to "the sucking of a sugar stick by a sweet-toothed infant".[109] Borers even reputedly attacked hawsers.[110] In contrast to such damage, no reports of borer action along the South Island West Coast surfaced, suggesting the success of improvements such as that to Jackson Bay jetty, which used muntz-metal sheathing (a combination of copper and zinc). This illustrates how resistant methods were becoming standard practice, regardless of the location and known presence of borers.

Science, identification and continued destruction, 1880s-1890s

In the 1880s, the first scientific report on woodborer damage appeared in New Zealand. Read before the Philosophical Institute of Canterbury, Charles Chilton identified gribbles and pillbugs amongst new crustacean discoveries. In 1882, he noted that the genus *Limnoria* (gribbles), and specifically *Limnoria lignorum*, was new to New Zealand and introduced from Europe.[111] Around the same time, the curator of Auckland Museum, Thomas Cheeseman, reported on the Mollusca around Auckland, remarking that *Teredo antarctica* was "boring into piles; much

---

[107] *SAR,* 4 May 1876, 6; *The West Australian (WA),* 3 Sep. 1880, 2.
[108] *Poverty Bay Herald (PBH),* 7 Aug. 1880, 2; *Timaru Herald (TH),* 20 Dec. 1888, 3.
[109] *TH,* 24 Jan. 1889, 2.
[110] *Manawatu Standard: Local and General,* 12 Mar. 1883, 2.
[111] Charles Chilton, 'Further Additions to our Knowledge of the New Zealand Crustacea', *Transactions and Proceedings of the Royal Society of New Zealand 1868-1961* 15 (1882): 69—86.

too abundant".[112] Currently regarded as 'nomen dubium', confusion behind this species' taxonomic status still exists.[113]

In this decade of further destruction and improved identification, timber choice remained the main measure taken against marine borers. While stone piling was an obvious material impervious to wood borers, it was very costly and time consuming to implement; only one site in Timaru utilised this.[114] The continued ineffectiveness of Australian timbers focused attention on New Zealand woods. In January 1883, a twenty-year-old Dunedin jetty presented sound Mānuka (*Leptospermum scoparium*) piles, indicating resistance to attack.[115] Tawa (*Beilschmiedia tawa*) also showed promise—a report on its beneficial properties for marine construction included durability from a young age and resistance to marine-borers.[116] Kauri's properties appeared promising, but Kauri bracing of Timaru wharf revealed severe gribble attack just one year after its recommendation.[117] In the same year, despite its many failures in preventing shipworm ravages, the Harbour Commissioners of San Francisco, California, trialled Kauri in marine construction, although the results are not known.[118] Despite its known susceptibility to borer in locations such as Auckland, Kauri was still being utilised in the construction of the Napier harbour bridge, possibly due to its availability and lower cost compared to imported varieties.[119]

---

[112] Thomas F. Cheeseman, 'On the Mollusca of the Vicinity of Auckland', *Transactions and Proceedings of the Royal Society of New Zealand 1868-1961* 19 (1886): 161—174.
[113] Turner, *A Survey and Illustrated Catalogue*, 9—13.
[114] *TH*, 17 Jan. 1889, 4.
[115] *Otago Witness*, 13 Jan. 1883, 7.
[116] *GRA*, 7 Jul. 1886, 2.
[117] *TH*, 20 Dec. 1888, 3.
[118] *Daily Alta California: Afloat and Ashore*, 7 May 1887, 4.
[119] Saunders, Douglas, Kelly, Pharazyn, 'Civil Service of New Zealand (Report of the Royal Commission Appointed to Inquire and Report upon the)', *Journals of the House of Representatives* H-02 (1880): 3—19.

Government also undertook a more thorough analysis of the benefits of chemical preservation. Correspondence between W. W. Evans in New York, an agent acting for the New Zealand government, and the New Zealand Under-Secretary for Public Works, on five patented chemical processes utilizing mixtures of tar, chloride of mercury, sulphate of copper, zinc and calcium took place in 1881. Evans' concluding remarks give the impression that creosoted American timbers, Palmetto (*Sabal palmetto*) and Greenheart (*Chlorocardium rodiei*), successfully resisted borers.[120] Perhaps due to the unavailability of these specific timbers, and the high costs of the creosoting process, New Zealand continued to pursue native timber alternatives.

In the mid-1880s, the comparison between Australian and New Zealand timbers resurfaced in Western Australian newspapers. In the *Western Mail* of 1886, an annual report by Wellington's Harbour Board engineer highlighted Tōtara's greater borer-resistance than Australian timber. The increasing damage to the three-year-old Jarrah sheathing along Wellington's Waterloo Quay breastwork added to the preference for native timber in New Zealand, noted the report, but wounded the pride of Western Australians.[121] *The Western Mail* pooh-poohed criticism of Jarrah, noting that:

> the alleged failure of our Jarrah timber to resist the attack of the Teredo need not unnecessarily disturb our equanimity, much less destroy our faith in the capabilities of our native mahogany. There are many posts and piles of that wood which are known to have been 35 or 40 years in water, which still remain apparently as sound at heart as when first put in.

[120] W. W. Evans, 'Process for Preserving Timber', *Journals of the House of Representatives* H-26 (1881): 1—10.
[121] *Western Mail (Perth, WA: 1885-1954) (WM),* 1 May 1886, 17.

Western Australia clearly regarded the Wellington Jarrah as a singular to the "remarkable durableness" of that timber.[122] Yet its findings also ignored several Australian studies of the 1870s highlighting Jarrah's ineffectiveness and inability to last longer than ten years when subject to attack.[123]

Borer destruction continued to spread around New Zealand in the 1890s (Fig 2). The destruction of several piles of Parua Bay's wharf significantly disrupted commerce in Whangarei.[124] "Serious Damage" occurred to the outer pier of the Opunake jetty, washed out to sea following shipworm destruction.[125] Construction of this pier had only finished in February 1892, making it just over two years old, and illustrating the speed at which borers work (Fig 3).[126] Further destruction continued in Timaru, and on Auckland's Queen's Street wharf while Napier wharf was described as being "endangered" by the Toredo.[127]

Figure 3 The first Opunake wharf constructed by 1892. Source: Puke Ariki, New Plymouth (PHO2011-0011).

---

[122] *WM*, 1 May 1886, 17.
[123] *Proceedings of the Royal Society of Tasmania*, Jul. 1874, 2; *West Coast Times*, 14 Jul. 1871, 2; *AS*, 5 Oct. 1876, 2.
[124] *Northern Advocate*, 12 Mar. 1892, 2.
[125] *Hawera and Normanby Star*, 25 Apr. 1894, 3.
[126] Margaret de Jardine, *The Little Ports of Taranaki* (New Plymouth: Margaret de Jardine, 1992), pp. 129—130.
[127] *Auckland Star (AS)*, 8 May 1893, 2; *Star*, 28 May 1898, 4; *TH*, 19 Oct. 1895, 2; *Tupeka Times* 3 Jun. 1891, 6.

There was little mention of any progress towards finding solutions to marine borer damage over the next few decades, despite their continued depredation on marine infrastructure. Constructed only six years earlier, by 1918, a wharf in Nelson was in a 'state of collapse' due to the ravages of shipworm.[128] Four years later, an *Evening Post* article reported a break in the Cook Strait cable, one of the six telegraph cables connecting the New Zealand's North and South Islands. Although initially attributed to *Teredo*—a species thought new to the region—a gribble species had actually inflicted the damage. Fortunately, the remaining cables coped with the extra communication traffic, whilst 'special measures to prevent borer' were considered.[129] Soon after his inspection of a piece of gutta-percha from the cable,[130] Charles Chilton attributed the damage to a non-indigenous gribble, *Limnoria lignorum*, rather than the maligned *T. navalis*.[131] Ongoing issues included piles in Tauranga collapsing into the harbour in 1923, and destruction to numerous Auckland wharves from the late 1920s to 1935.[132]

Concrete solutions

Recognition of the impacts of gribbles increased from the 1920s, due to increasing scientific understandings of their presence and identification. One instance at St. George's Bay boat skidways, Auckland, involved an estimated ₤1200 worth of gribble damage.[133] Greater awareness of existing borer-resistant techniques also developed in the twentieth century. In 1905, the Thames Harbour Board, New Zealand, sought advice on infrastructure improvements from Sir John Coode, an

---

[128] *Evening Post (EP)*, 5 Feb. 1924, 5.
[129] *EP*, 20 Jul. 1916, 2.
[130] Gutta-percha is a hard natural latex material produced from the sap of tropical trees in the genus *Palaquium*
[131] Charles Chilton, 'XX.-The Gribble (*Limnoria lignorum*, Rathke) Attacking a Submarine Cable in New Zealand', *Journal of Natural History Series 8* 18 (1916): 208.
[132] *AS*, 22 Jan. 1923, 7; *AS*, 12 Aug. 1935, 5.
[133] *AS*, 29 Mar. 1923, 8. 'The latter named borer, although scarcely larger than a grain of rice, is as destructive as the Teredo'; *AS*, 31 Aug. 1927, 9.

English civil engineer and a leading figure in harbour construction. He recommended the use of Tōtara and Mataī, and elimination of sapwood in marine construction.[134] The testing of ferro-concrete piles began in Auckland and Napier in the early 1900s,[135] and following success, became a common material used in wharf construction.[136] In 1907-1910, Wellington's Clyde Quay was constructed of ferro-concrete,[137] replacing Auckland's dilapidated timber-constructed Kings wharf in 1908.[138] Several other locations around the country replaced wooden wharves with those made from ferro-concrete.[139] Aside from anticipated on-going maintenance, the ferro-concrete wharves remain in place today, demonstrating the main advantage over timber; long-term persistence.

Although concrete's main advantage over timber was that it presented a viable long-term option, research into alternative borer-resistant woods continued, including that undertaken by the newly-formed State Forest Service; an organization with a clear vested interest in encouraging continuing timber usage. A Forest Service engineer, R. Entrican, described additional native trees resistant to marine woodborers, including Kohekohe (*Dysoxylum spectabile*) and Pukatea (*Laurelia novae-zelandia*), which had ideal properties for boat building.[140] The naturally resistant Pōhutukawa (*Metrosideros excelsa*), provided another alternative for defence against borer ravages.[141] On the other hand, Wellington Harbour Board chose to utilize Australian Turpentine for the Miramar Wharf

[134] *Thames Star*, 13 Sep. 1905, 4.
[135] Ferro-concrete is reinforced with a core of iron or steel.
[136] *PBH*, 31 Aug. 1904, 2; *Marlborough Express*, 23 Mar. 1906, 2.
[137] John McLean, 'McLean, Neil', *Dictionary of New Zealand Biography* 3(1996): 11.
[138] *NZH*, 13 Jun. 1906, 7.
[139] *NZH*, 13 Apr. 1908, 6; *ODT*, 10 Oct. 1907, 2.
[140] *EP*, 31 Aug. 1926, 2.
[141] *Otago Witness*, 21 Dec. 1904, 76.

extension in 1923, following its successful borer resistance in Sydney Harbour, when erected with its bark intact.[142]

Interest in overseas preservation techniques also continued. British engineers identified the impregnation of arsenic into timber as the most successful option for resisting shipworms, and creosote the best option for gribbles.[143] In 1933, Dr. Sonti Kamesam, a timber engineer from India, invented chromium, copper and arsenic (CCA) for timber prevention against insects, fungi and marine borers, and received a British patent.[144] New Zealand began to utilise CCA in the 1950s and remains one of the largest users of this preservative, including for the treatment of marine pilings.[145] This is despite recent research indicating neither creosote nor CCA are infallible to pillbugs and gribbles.[146]

Conclusion

As this article demonstrates, ever since transoceanic exploration, migration and trade opened up material opportunities and intellectual horizons for human-kind several thousands of years ago, human ocean-going travellers have been accompanied—and challenged—by marine wood borers. For millennia, marine woodborers have had an important, if largely unacknowledged, impact on the social, economic and political history of the world, particularly after 1800, following the unprecedented growth in volumes of shipping. Until the 1860s, most of this travel relied on wooden-built ships. Even with the later development of iron steam-ships, wooden vessels continued their importance as a means of

---

[142] *EP: To Deepest Water*, 29 Aug. 1923, 6.
[143] *EP*, 25 Jun. 1936, 26.
[144] Environmental Risk Management Authority (hereafter ERMA), *Report on Copper, Chromium and Arsenic (CCA) Treated Timber*, by Deborah Read. ISBN 0-478-21521-5 (Wellington: ERMA, 2003): 7.
[145] ERMA, *Report*, 7.
[146] S. M. Cragg, A. J. Pitman, S. M. Henderson, 'Developments in the Understanding of the Biology of Marine Wood Boring Crustaceans and in Methods of Controlling them', *International Biodeterioration and Biodegradation* 43(1999): 197—205.

transportation. Meanwhile, wooden marine infrastructure, principally in the form of jetties, wharves and bridges, played a crucial role in supporting the thriving trade and economy of places like New Zealand, connected with ever greater frequency to international shipping networks.

These shipping networks, this article argues, inadvertently led to the introduction of a host of marine wood borers, whose impacts became evident in New Zealand from the 1860s. Thereafter, they caused widespread damage to marine infrastructure up and down the country, disrupting New Zealand's growing export economy and playing havoc with many local port authorities. International and domestic research, as well as the trialling of local and overseas timbers, often provided the foundation for New Zealand's management attempts, with repetition of the same techniques occurring over several decades until the more widespread and successful use of ferro-concrete pilings from the 1900s. This lengthy failure to learn from the past, and a lack of co-ordinated research into preservation techniques and timber alternatives, may indicate the fragmentation of colonial knowledge, as international ideas were introduced at a local rather than nation level.

When considered within a global context, an outline of New Zealand's past damage and responses acknowledges the significant role of woodborers in marine environmental history. The historical persistence of their impact, and the seemingly endless process of human trial and error to manage them, is surely testament to their deserved significance and attention in environmental history.

Chapter III

Genetic diversity and structuring of marine wood borers in New Zealand; can native and non-indigenous species be differentiated?*

*To be submitted for publication under the same title as: Rayes CR, Duggan IC, Hogg ID.

Abstract

Known for the significant destruction they inflict on marine infrastructure, marine wood borers present a major worldwide concern. In New Zealand several marine wood borers are considered non-indigenous or are of uncertain origin. Although assumed to have invaded New Zealand via wooden ships, introductions are historic, and it is possible that some were present in New Zealand prior to human colonization. We used analyses of mitochondrial DNA (COI) to examine population genetic structuring, species diversity and taxon relationships among New Zealand borer species, to elucidate their status as native or non-indigenous. Low levels of genetic divergence (0-2%) were found among the New Zealand populations of the isopods *Limnoria quadripunctata* and *Sphaeroma quoianum*, while *L. quadripunctata* also showed a strong genetic affinity to a population in Chile, suggesting a non-indigenous status. Population genetic structuring among *L. quadripunctata* populations showed geographic patterns consistent with that commonly described for native New Zealand species, although with lower genetic diversity; this pattern may be explained by independent introductions to different ports through time. For the shipworm *Lyrodus pedicellatus*, a lack of genetic affinity to conspecifics sequenced elsewhere (France), greater genetic diversity compared to the native *Bankia australis*, and evidence of population genetic structuring among New Zealand locations, suggests *L. pedicellatus* may be native to New Zealand. *Lyrodus pedicellatus* population structuring was also consistent with the degree of divergence found for native molluscan species around New Zealand. Our findings suggest past evaluation of wood borers' status have overlooked their historical dispersal. Molecular genetics provides a useful tool for status re-evaluation.

Introduction

Marine wood borers play a significant role within marine and estuarine ecosystems. Through the break-down of woody debris they facilitate nutrient cycling and energy turnover (Santhakumaran 2003). They also assist in mangrove forests by promoting aerial root growth and are known to shape the lower intertidal limits of mangrove forests (Simberloff et al. 1978; Svavarsson et al. 2002). Accordingly, they are a significant component of the natural biodiversity for some marine ecosystems (Santhakumaran 2003; Cannicii et al. 2008). However, wood borers are also responsible for worldwide damage to marine infrastructure and infestation of wooden vessels (Cobb 2002; Distel et al. 2011). Despite efforts to develop effective timber preservatives, borer damage remains a significant issue for marine infrastructure and submerged wrecks, with the continued spread of species to new regions (Björdal et al. 2012; Borges et al. 2012).

The majority of marine wood borers are from two taxonomic classes and represented by three key families, Teredinidae (Mollusca; Bivalvia), and Limnoriidae and Sphaeromatidae (Arthropoda; Isopoda) (Miller 1926; Cragg et al. 1999; Paalvast & van der Velde 2011; Chapter 1). A variety of dispersal vectors exist for marine wood borers, including boat hulls and driftwood for adults, and drift and shipping ballast water for larvae (McKoy et al. 1980; Hayden et al. 2009). The widespread modern distributions of many borer species are thought to have primarily resulted from their historical movement in the hulls of wooden ships (Pillai 1965; McKoy 1980; Minchin et al. 2009). The historic nature of dispersal has resulted in unknown timings of introduction and questionable native ranges for several species, making it challenging to distinguish between native or non-indigenous status (Carlton 1987; Cranfield et al. 1998). Some species currently considered 'introduced' may in fact be native, while those considered native may similarly constitute recent introductions. Carlton (1999) suggested the need to reconsider presumed 'naturally cosmopolitan' species, including teredinid species, as they potentially represent introductions from early colonisation. The clarification of a species' status in a given region would allow for a greater understanding of the ecology, biogeography and human impact patterns (Carlton and Geller 1993), and provide a foundation for the conservation of natural biodiversity.

Knowledge of a species status in a given region is essential for understanding the fundamental aspects of historical marine invasions such as species origins and transportation pathways (Carlton 1996; Fofonoff et al. 2003). Chapman and Carlton (1991) outlined criteria for distinguishing native from introduced species. Among these, key criteria include: 1) association with human mechanisms of dispersal; 2) prevalence or restriction to new or artificial environments; 3) restricted distribution compared to native species; and 4) morphological and genetic affinities to elsewhere in the world (Chapman and Carlton 1991). However, such criteria may be considered poor indicators for distinguishing non-native borers, due to the lack of known origins or date of introduction. In addition to their natural mangrove habitats and association with driftwood, wood borers are common on anthropogenic substrates and are associated with human-mediated vectors regardless of whether they are native or introduced.

Molecular data such as DNA barcoding (*sensu* Hebert et al. 2003) may provide an additional tool to assess the invasion-status for taxa. Specifically, by examining population genetic structure, species diversity and taxon relationships, we can test hypotheses related to the questionable invasions and native ranges of marine species (Sakai et al. 2001; Blakeslee et al. 2008). In particular, molecular techniques have proven to resolve cryptogenic histories of marine species, where their native or non-indigenous status cannot be distinguished (Blakeslee et al. 2008). Borges et al. (2012) also suggested the future use of molecular genetics to identify non-native and cryptic borer species.

Introductions of marine species to New Zealand are thought to have occurred since European colonization in the nineteenth century, and potentially prior to this with Māori settlers since ca. 1300 (Hayden et al. 2009). Regardless of New Zealand's relatively short human history, non-indigenous marine species pose a significant threat from both an ecological and economical perspective (Hayden et al. 2009; Ahyong and Wilkens, 2011). During early European exploration and colonisation there would have been ample opportunity for introductions via wooden ships. Cranfield et al. (1998) compiled a list of non-indigenous marine species in New Zealand, using the criteria of Chapman and Carlton (1991), and inferred several marine wood borer species to be non-indigenous. The accurate assessment of the status of these marine wood borers, native or non-indigenous, is debatable and requires clarification. The unknown and historical nature of introductions and lack of 'probable' native ranges have also not been addressed (Carlton 1996; Cranfield et al. 1998). Therefore, investigation into New Zealand wood borer species is required to verify their native or non-indigenous status.

The cytochrome *c* oxidase subunit I gene (COI) has been used in New Zealand to examine the intra- and inter-specific genetic divergences and geographical structuring of New Zealand's marine taxa (e.g. Hickey et al. 2009; Knox et al. 2011, Ross et al. 2012), as well as to clarify species' status (e.g. Stevens et al. 2002). Many native coastal marine species show clear genetic structuring influenced by oceanic currents around New Zealand, including genetically divergent regions of the East Cape, Cook Strait and East/West coasts of the North Island (Ross et al. 2009; Fig 1.). Natural dispersal across these regions has been limited by barriers, including land, and the boundaries of current systems and eddies, which restrict connectivity between populations (Chapman and Carlton 1991; Ross et al. 2009). Intraspecific divergence values associated with genetically divergent geographic regions for native species around New Zealand include a range of 4.6-8.3% for crustaceans and 0.3-2.0% for molluscs (Goldstien et al. 2006; Knox et al. 2011). Such studies provide levels of divergence for comparison with the genetic structuring in borer species', providing evidence for their native or non-indigenous status. On a larger scale, the availability of global sequence databases (e.g. BOLD; Ratnasingham et al. 2007) can place New Zealand borer species into a wider geographical framework to examine the genetic affinities to borers elsewhere in the world.

In this study we investigated the status, spatial distribution and genetic diversity of Teredinidae, Limnoriidae and Sphaeromatidae species collected from wooden substrates around the North Island, New Zealand. We tested the hypotheses that North Island non-indigenous wood borers would be: 1) limited to regions surrounding historically important ports; 2) present less genetic structuring and have more restricted geographical distributions compared to native species; and 3) have greater genetic affinities with those collected from other regions of the world. In doing so, our aim was to assess the native or non-indigenous status of New Zealand marine wood borers.

Methods

The New Zealand taxa

New Zealand Teredinidae (Mollusca) include three species considered non-indigenous; *Lyrodus medilobatus*, *L. pedicellatus* and *Nototeredo edax*, and two native; *Bankia australis* and *B. neztalia* (McKoy 1980; Cranfield et al. 1998). The three non-indigenous species have a probable tropical cosmopolitan native range, and the two native species extend to temperate-cool waters. However, all occur widely in New Zealand harbours (Cranfield et al. 1998; McKoy 1980). Of the isopod taxa, two limnoriid species, *Limnoria quadripunctata* and *L. tripunctata*, are considered non-indigenous, although lack a known origin or date of introduction (McQuire 1964; Schotte 1989; Cranfield et al. 1998). *Limnoria tripunctata* has a restricted distribution, as might be expected of a non-indigenous species, known only from Auckland Harbour, whereas *L. quadripunctata* is widely distributed in New Zealand harbours (McQuire, 1964). For the Sphaeromatidae, *Sphaeroma quoyanum* is considered a New Zealand native by Davidson et al. (2008), although non-indigenous by Johns (2010). Johns (2010) considered *Sphaeroma laurensi* native to New Zealand, and it is only known in one east coast location; Gisborne (Hurley and Jansen 1977; Johns 2010).

Study area

Seventeen harbour locations were selected around the North Island, New Zealand, based on pre-1900 trading ports, shipping patterns, and to represent major current zones (Rimmer 1967; Hayden et al. 2009; Ross et al. 2009) (Fig 4). Two sites at each location were visited in January and July 2013 to attach and remove sampling equipment. Sampling sites were selected based on the presence of submerged wooden structures in each harbour, and sites included intertidal marine and estuarine habitats.

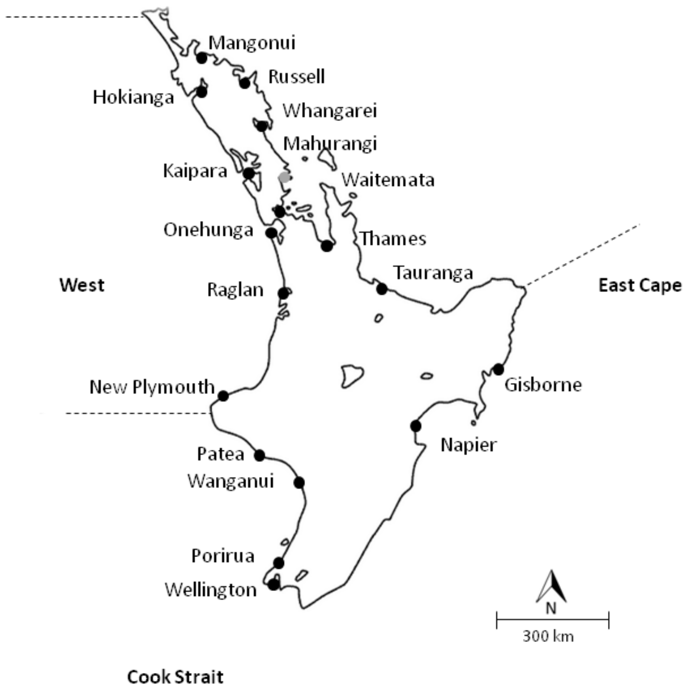

Figure 4 Sampling locations for marine wood borer in New Zealand. The Mahurangi river location represents an additional collection site for Sphaeromatidae specimens only. Bold titles represent genetically divergent regions and dotted line represents the natural boundary bioregions based on Shears et al. (2008) and Ross et al. (2009).

Sample Collection

Constructed wooden sampling ladders (Fig 5) were used to collect marine wood borers at each site. Ladders consisted of four untreated *Pinus radiata* panels (8 x 2 cm section x 20 cm length), two rough-sawn and two planed smooth, bolted to a *Pinus radiata* backbone (4.5 x 2 cm section x 63 cm length) treated with creosote and copper chrome arsenic (H4). Two ladders were attached to the intertidal zone of timber pilings in each harbour, using galvanized steel coach screws (W: 8, L: 75). Where possible, pilings were selected based on existing wood borer damage and ease of access. Ladders were attached above water, leaving them fully immersed at high tide.

The ladders were removed after six months (Fig 5), dismantled, and the surfaces scraped free of marine growth. Panels were then inspected for borer entrances, and split open using a chisel and hammer. A scalpel and forceps were used to carefully scrape open the tunnels and remove any borers. Fully intact specimens of isopods (Limnoriidae and Sphaeromatidae) were removed. However, due to the extensive tunnels formed by the Teredinidae, only some specimens were fully intact—the remainder consisted of an intact posterior or anterior section and portions of the of the body. The isopods and molluscs were preserved separately in 95% ethanol, and transported back to the laboratory for identification and further processing.

All specimens were identified to the lowest taxonomic level possible using the illustrated guides of Turner (1966) (Teredinidae), Hurley and Jansen (1977) (Sphaeromatidae), and Cookson (1991) (Limnoriidae).

Figure 5 Constructed wooden sampling ladders before deployment and after the six month deployment period.

Table 2 Harbour locations sampled for marine wood borers around the North Island, New Zealand. Plus and minus signs represent species presence and absence.

	Presence/Absence		
Harbour	**Mollusca Teredinidae**	**Arthropoda Limnoriidae**	**Arthropoda Sphaeromatidae**
Mangonui	+	+	-
Russell	+	+	-
Hokianga	+	+	-
Kaipara	+	-	-
Whangarei	+	+	-
Mahurangi	-	-	+
Waitemata	+	+	+
Onehunga	+	+	-
Thames	-	-	+
Tauranga	+	+	+
Napier	-	+	-
Gisborne	+	-	-
New Plymouth	+	+	-
Porirua	-	+	-
Wellington	-	-	-

Genetic Methods

Genetic analyses were performed at the University of Waikato and at the Canadian Centre for DNA Barcoding (CCDB) at the University of Guelph. University of Waikato DNA extractions were carried out using REDExtract-N-Amp Tissue Kits according to manufacturer's guidelines, with the only modification being a longer incubation period of 2-3 hours at room temperature (Sigma-Aldrich Co.). Polymerase Chain Reactions (PCR's) using a 15 µl reaction volume consisting of 1µl of DNA, 5.5 µl Milli-Q water, 7.5µl Blue Juice™ loading buffer (Life Technologies Co.) and 0.5 µl of each primer were undertaken at the University of Waikato. CCDB PCR's were comprised of 12.5 µl reaction volumes including 2µl DNA, 6.5 µl 10% trehalose, 2 µl ddH_2O, 1.25 µl buffer (10x), 0.625 µl $MgCl_2$, 0.125 µl of each primer, 0.0652 µl dNTPs and 0.06 µl polymerase. All PCR runs included a positive (previously successfully amplified sample) and a negative control (distilled water). A 658 bp fragment of the COI gene was amplified using the primer pair HCO2198 (5'TAAACTTCAGGGTGACCAAAAAATCA-3') and LCO1490

(5'-GGTCAACAAATCATAAAGATATTGG-3') (Folmer et al. 1994). At the CCDB the primer pair BivF4_t1

(5'-TGTAAAACGGCCAGTGKTCWACWAATCATAARGATATTGG-3') and BivR1_t1

(5'-CAGGAAACAGCTATGACTAMACCTCWGGRTGUCCRAARAACCA-3')

(BOLD Systems, Sean Prosser unpublished) was used. PCR thermal cycling conditions at the University of Waikato were: 5 min at 94°C; 36 cycles of 1 min at 94 °C, 1.5 min at 52 °C and 1 min at 72°C; and 5 min at 72°C on an Eppendorf® Mastercylcer® gradient thermocycler. Thermal cycling conditions at CCDB were: 1 min at 94°C; 5 cycles of 30 sec at 94 °C; 40 sec at 45-50°C; 1 min at 72°C; 30-35 cycles of 30 sec at 94°C; 40 sec at 51-54°C; 1 min at 72 °C; and 10 min at 72 °C on an Eppendorf® Mastercycler® ep gradient thermocycler. University of Waikato PCR products were electrophoresed (64 volts, 30 min) on a gel of 30 ml TBE, 300 µg agarose and 3 µl SYBR® Safe DNA gel stain (Life Technologies Co.), and visualized under UV light. CCDB electrophoresed PCR products on Invitrogen™ pre-cast agarose gels for 6-12 min using the Mother E-BASE™ (Ivanova & Grainger, 2014).

PCR products were cleaned using 0.2 µl EXO, 0.1 µl SAP and 2.7 µl Milli-Q water at the University of Waikato. Thermal conditions were 30 minutes at 37 °C and 15 minutes at 80 °C. Purified PCR products were sequenced on an AB13130 sequencer at the University of Waikato DNA sequencing facility using the same amplification primers. CCDB sequences were obtained using an ABI 3730xl DNA Analyzer (Applied Biosystems Inc.) using the sequence primer pair M13F (-21) (GTAAAACGACGGCCAGT) and M13R (-27) (CAGGAAACAGCTATGAC) (Messing, 1983). All specimen details were uploaded to the Barcode of Life Datasystems (BOLD) database (www.boldsystems.org) under project NZBOR.

Genetic Analyses

Sequences were aligned and edited using Geneious (R7 ver. 7.0.4 for Macintosh), and verified using the GenBank BLAST algorithm and BOLD database sequence searches. Sequences for isopods and molluscs were analyzed separately. We obtained 57 New Zealand isopod sequences, and acquired additional sequences from BOLD and GenBank (23 Limnoriidae and 18 Sphaeromatidae), as well as three arthropod sequences to serve as outgroup taxa. Outgroups represented three different isopod families; Cymothoidae, Idoteidae and Phreatoicidae (GenBank accession numbers; KC428828.1, FCFC039-04 and FCFC051-04). The molluscs included 19 North Island Teredinidae sequences, as well as 31 further Teredinidae sequences sourced from BOLD or GenBank. Two bivalve molluscan species (*Pholas orientalis* and *Barnea candida* GenBank accession numbers; JQ267793.1 and KC429152.1, respectively), were used as outgroup taxa.

For both alignments Chi-squared tests were performed using PAUP* (ver.4b10-x86-macosx) (Swofford 2002) to test the assumption of equal base frequencies for all codon positions, and for third codon positions only. Neighbor-joining (NJ) phylograms were constructed using Molecular Evolutionary Genetics Analysis

(MEGA) software (ver.5.2 for Windows) (Tamura et al. 2011). These were conducted using the phylogeny test, Bootstrap (1000 replications) method, to give a level of confidence in cladistic results, and Kimura-2-parameter (K2P) model (Kimura 1980). All other options in MEGA remained as default. The jModelTest 0.1.1 (Guindon and Gascuel 2003; Posada 2008) was used to determine the best-fit model for maximum likelihood (ML) searches. The optimum model output for both the isopods and molluscs was GTR+I+G (-lnL: 491.3524 and -lnL: 4536.8929). ML phylograms were constructed in MEGA using this model output and the remaining default settings for both alignments.

Bayesian inference: BEAUti (ver.1.7.5) (Drummond and Rambaut 2007) was used to create a BEAST xml file for both alignments. Within BEAUti the following parameters were used for all analyses: partition - COI; sites - substitution model GTR+I+G gamma with 4 categories; clock - log normal relaxed (uncorrelated) distribution; trees - speciation: Yule process and priors - lognormal. The remaining parameters stayed as default settings.

Bayesian analyses of the two alignments were performed using Bayesian Evolutionary Analysis Sampling Trees (BEAST ver.1.7.5) (Drummond and Rambaut 2007). Results were visually analyzed in Tracer (ver. 1.5) (Drummond and Rambaut 2007). Upon confirmation of a successful run, Tree Annotator (ver. 1.7.5) (Drummond and Rambaut, 2007) was used to visualize posterior probabilities (PP) from the resulting sample of trees. Tree Annotator used the default setting of 10% (1000) burn in producing a sample of 10000 trees. The Bayesian majority rule tree was visualized using Fig tree (ver. 1.4.0).

Sequence divergences were calculated using the K2P model in MEGA. Distances within and between groups of species and locations were averaged for comparison.

Results

Isopoda

Limnoriidae specimens were collected from ten sites, and Sphaeromatidae specimens from only four (Table 2). A 592 base pair fragment of the COI mitochondrial gene was used for the isopod analyses. Of the 592 characters, 92 were constant, 40 variable parsimony uninformative, and 460 parsimony informative. When using the third codon position only, 395 characters were excluded and 197 included. The average nucleotide composition across all isopod sequences was, A = 22.5%, T = 35.5%, C = 18%, G = 24%, revealing a slight A-T bias. The assumption of homogeneity of base frequencies among sequences was supported using all codon positions (χ^2 = 140.25, P = 1.00, df = 300), and for the third codon position only (χ^2 = 246.79, P = 0.99, df = 300).

All tree construction methods (NJ, ML and Bayesian) separated the Limnoriidae from the Sphaeromatidae, and species and location groupings were consistent between trees. Only the ML and Bayesian are shown (Fig 6 and 7). The majority of the groupings were well supported with bootstrap analysis and posterior probability values.

Interspecies comparisons ranged from 30% between *Limnoria quadripunctata* and *Limnoria stephensensi* sequences. *Sphaeroma quoianum* sequences from the Waitemata, Thames and Mahurangi Harbours were 22 to 27% divergent to individuals from Tauranga, Honolulu and South Africa. Complete comparisons of sequence pairwise distances averaged within and between groups of Limnoriidae and Sphaeromatidae are provided in Table 3.

Intraspecific divergences ranged from 0 to 2% for the putatively non-indigenous *Limnoria quadripunctata* across the New Zealand and Genbank sequences. Napier and Chilean populations were the most divergent from others, and most closely related to each other, than were the other New Zealand populations (Table 3).

New Zealand populations of *Limnoria quadripunctata* sharing a common coastline generally grouped together, with East (Waitemata, Russell, Mangonui and Whangarei) and West (Hokianga, Porirua and New Plymouth) coast groups. Hokianga was also grouped separately to the remaining locations (Fig 7). Furthermore, the northern east coast sites, Mangonui, Russell, Whangarei, Waitemata, and Tauranga, were grouped separately to the more southern Napier population (Fig 7). The other *Limnoria* species (*L. stephensensi*) from the Subantarctic Islands were the most divergent amongst Limnoriidae sequences.

There was a clear division among New Zealand Sphaeromatidae, delineating two different genera and species. Six *Sphaeroma quoianum* from northern east coast populations were grouped separately to the two *Exosphaeroma* cf. *obtusum* (not typically considered a wood borer) from Tauranga. Interspecific divergence between the two New Zealand species was 23%, with *Exoshpaeroma* cf. *obtusum* from Tauranga as similar to *Cilicaea* sp. from Hawaii and *Exosphaeroma hylecoetes* from South Africa (Fig 6, Table 3). Overall, interspecies comparisons ranged from 22 - 28% between *Exosphaeroma* cf. *obtusum* and *Sphaeroma quoianum* from New Zealand and *Exosphaeroma hylecoetes* from South Africa. Little intraspecific divergence was present across New Zealand populations of *Sphaeroma quoianum*, with equal divergence between the three locations, Waitemata, Thames and Mahurangi (Table 3). Complete comparisons of sequence pairwise distances averaged within and between groups of Limnoriidae and Sphaeromatidae are provided in Table 3.

Figure 6 Enlarged portion of the Maximum likelihood tree for Sphaeromatidae and Limnoriidae families. Numbers beside some of the locations indicate the number of identical sequences in that particular group.

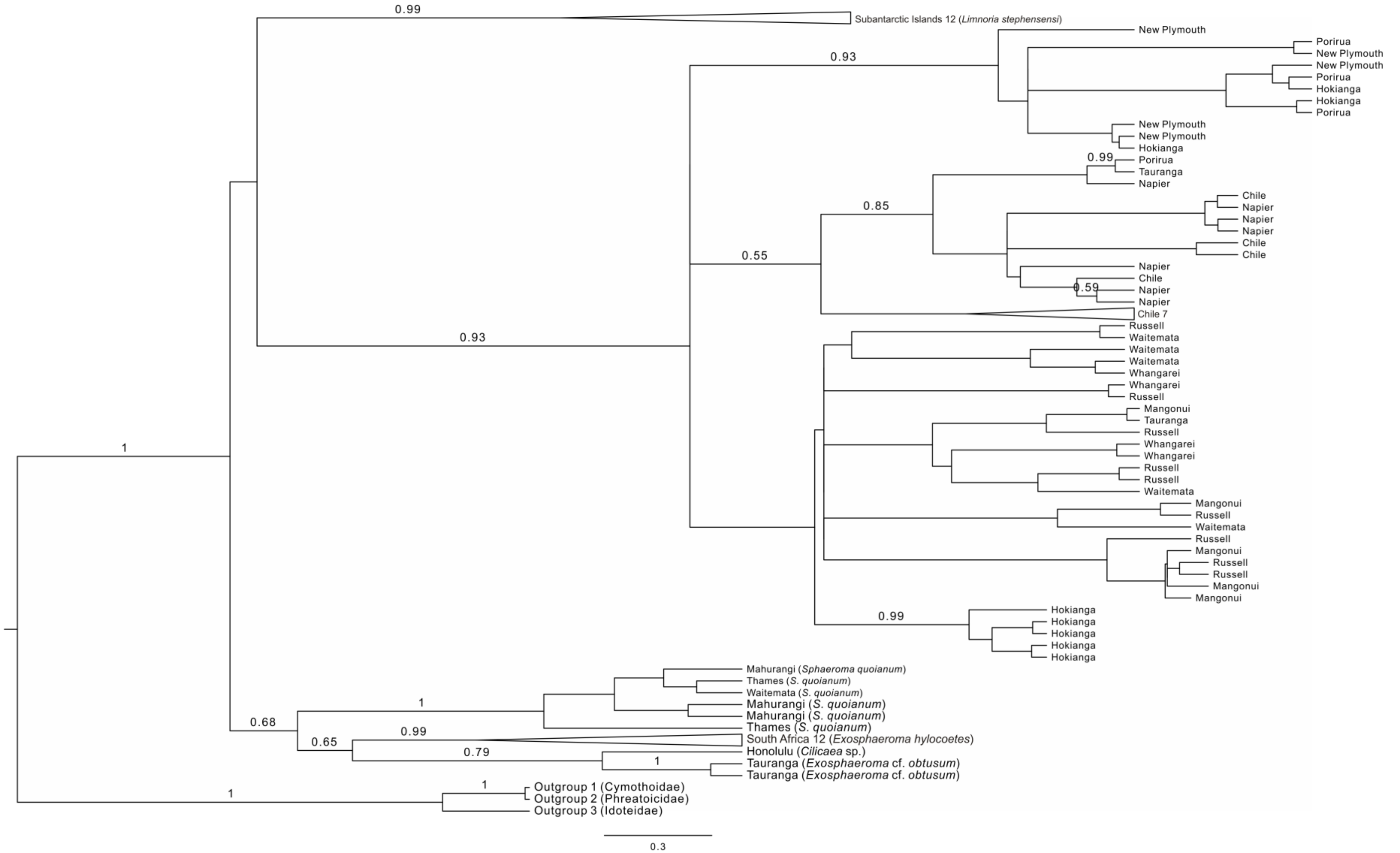

Figure 7 Bayesian majority rule probability tree for Limnoriidae and Sphaeromatidae families. Posterior probability values (PP) above 0.5 are indicated on the branches. Numbers beside some of the locations indicate the number of identical sequences in that particular group.

Table 3 mtDNA (COI) sequence pairwise distance values averaged between groups of Limnoriidae and Sphaeromatidae (Arthropoda: Isopoda) populations

Location (species)	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**
1.Hawaii (*Cilicaea* sp.)	0.00																
2.Tauranga (*Exosphaeroma* cf. *obtusum*)	0.23	0.00															
3.Waitemata (*Sphaeroma quoianum*)	0.23	0.26	0.003														
4.Mahurangi (*S. quoianum*)	0.23	0.26	0.003	0.002													
5.Thames (*S. quoianum*)	0.23	0.26	0.003	0.002	0.002												
6.South Africa (*Exosphaeroma hylecoetes*)	0.23	0.22	0.27	0.27	0.27	0.02											
7.Subantarctic Islands (*Limnoria stephensensi*)	0.34	0.35	0.32	0.32	0.32	0.36	0.00										
8.Chile (*Limnoria quadripunctata*)	0.33	0.38	0.35	0.35	0.35	0.39	0.3	0.00									
9.Waitemata (*L. quadripunctata*)	0.33	0.37	0.36	0.37	0.37	0.38	0.3	0.02	0.00								
10.Russell (*L. quadripunctata*)	0.33	0.37	0.37	0.37	0.37	0.38	0.3	0.02	0.00	0.00							
11.Hokianga (*L. quadripunctata*)	0.34	0.37	0.37	0.37	0.37	0.38	0.3	0.02	0.00	0.00	0.00						
12.Whangarei (*L. quadripunctata*)	0.33	0.37	0.36	0.37	0.37	0.38	0.3	0.02	0.00	0.00	0.00	0.00					
13.Porirua (*L. quadripunctata*)	0.33	0.38	0.36	0.36	0.36	0.38	0.3	0.02	0.00	0.00	0.00	0.00	0.01				
14.Napier (*L. quadripunctata*)	0.33	0.38	0.35	0.36	0.36	0.39	0.3	0.00	0.02	0.02	0.02	0.02	0.02	0.00			
15.New Plymouth (*L. quadripunctata*)	0.35	0.38	0.38	0.36	0.36	0.38	0.3	0.02	0.00	0.00	0.00	0.00	0.00	0.02	0.00		
16.Mangonui (*L. quadripunctata*)	0.33	0.37	0.36	0.36	0.37	0.38	0.3	0.02	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	
17.Tauranga (*L. quadripunctata*)	0.33	0.38	0.36	0.36	0.36	0.38	0.3	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.02

Mollusca

Teredinidae specimens were collected from ten sites (Table 2). A 553 base pair fragment of the COI mitochondrial gene was used for the mollusc analyses, which included 19 Teredinidae sequences from New Zealand, and 33 sequences obtained from GenBank and BOLD databases. Of the 553 characters, 217 characters were constant, 72 variable but parsimony uninformative, and 264 were parsimony informative. When using the third codon position only, 369 characters were excluded and 184 included. The average nucleotide composition across all mollusc sequences was, A = 22%, T = 33%, C = 18%, G = 29%, revealing a slight A-T bias. The assumption of homogeneity of base frequencies among sequences was supported using all codon positions (χ^2 = 140.25, P = 1.00, df = 153), and for the third codon position only (χ^2 = 8.77, P = 1.00, df = 153).

All tree construction methods (ML, NJ and Bayesian) distinguished between Teredinidae species, presenting similar topology. Only the ML and Bayesian are shown (Fig 8 and 9). Several of the larger clusters with more than one species lacked good support. Intraspecific groupings of New Zealand *Lyrodus pedicellatus* and the same species in France were not evident, suggesting geographical isolation, although there was little intraspecific population structuring when only considering New Zealand.

Interspecific sequence divergences are provided in Table 4. Interspecific divergences between New Zealand populations of teredinids and those of France and Turkey were between 21 - 44%. This included high interspecific divergence between populations of *Lyrodus pedicellatus* 24 - 25% and the *Bankia* genus 30%. Sequence divergences between New Zealand species ranged between 21 - 30%, with the two *Lyrodus* species showing the lowest divergence, and a lone

Teredinidae sp. individual from Tauranga the highest divergence from all others. This teredinid individual presented no genetic similarity to any other Teredinidae species, and could not be identified morphologically due to damage, to the pallets required for identification. Intraspecific divergences for New Zealand populations were ≤ 1%, with little genetic structuring among populations of the same species.

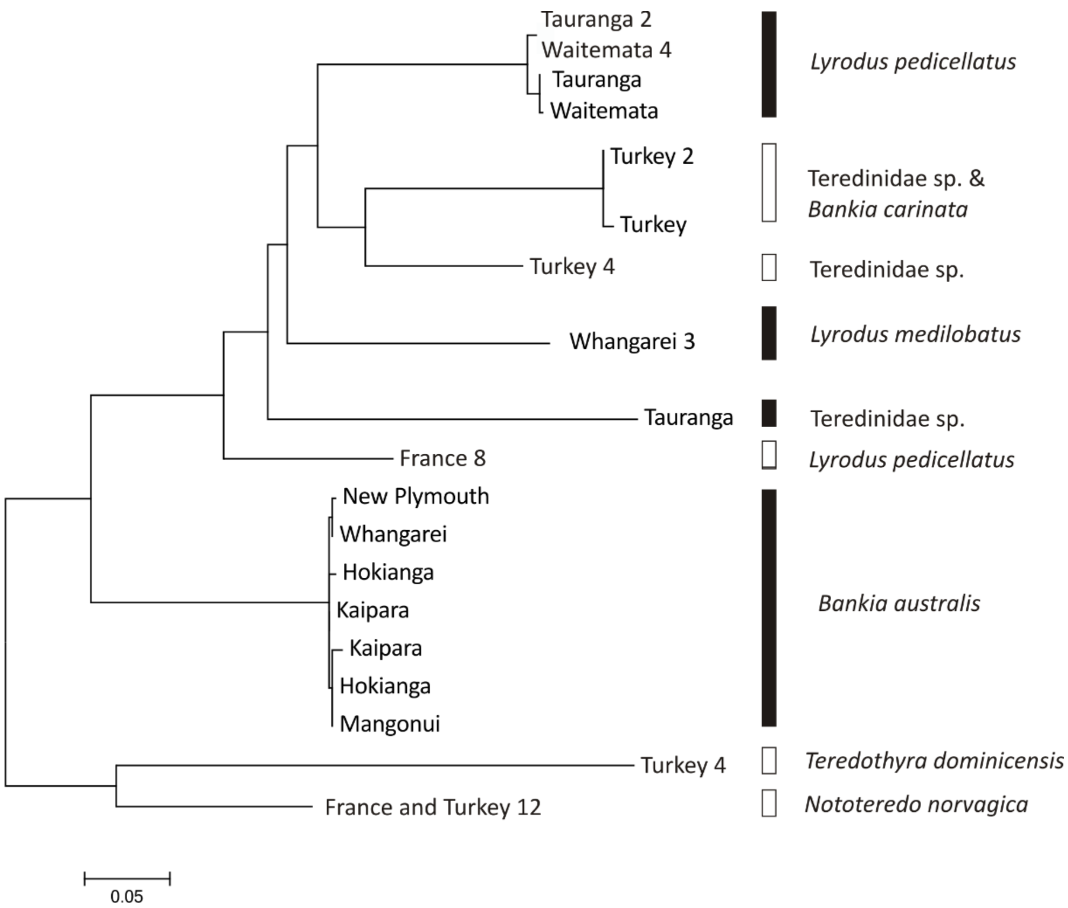

Figure 8 Enlarged portion of Maximum Likelihood tree for Genbank (white groups) and New Zealand (black groups) Teredinidae sequences. Numbers beside some of the locations indicate the number of individuals in that particular group.

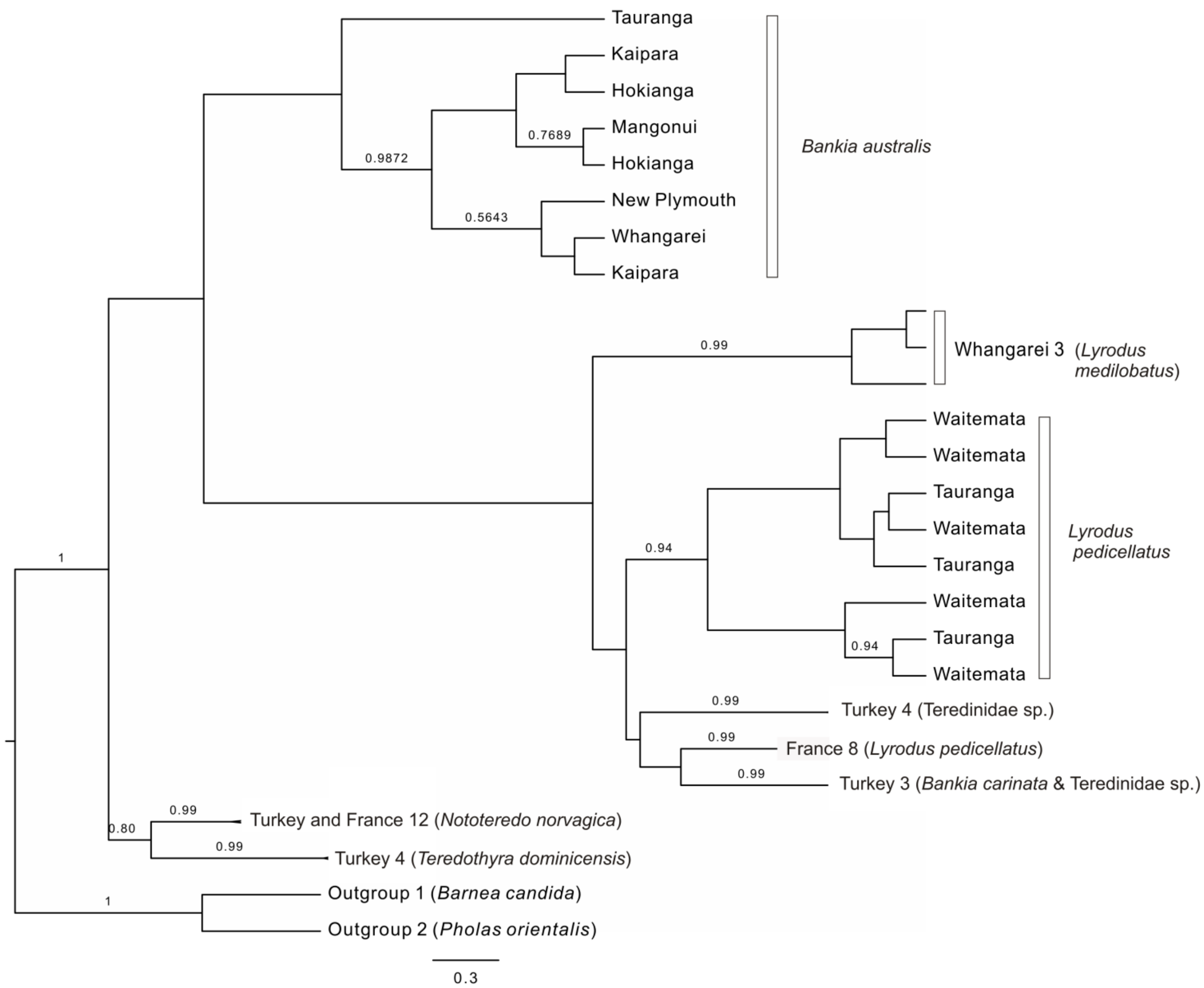

Figure 9 Bayesian majority rule probability tree for Teredinidae. Posterior probability values (PP) above 0.5 are indicated on the branches. Numbers beside some of the locations indicate the number of individuals in that particular group.

Table 4 mtDNA (COI) sequence average pairwise distance values using K2P. 1-4 populations from France and Turkey, 5-14 North Island, New Zealand populations.

Site (Species)	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1.Turkey/France (*Nototeredo norvagica*)	0.003													
2.Turkey (Teredinidae sp.)	0.22	0.23												
3. France (*Lyrodus pedicellatus*)	0.29	0.21	0.06											
4.Turkey (*Teredothyra dominicensis*)	0.31	0.36	0.38	0.00										
5.Turkey (*Bankia carinata*)	0.35	0.21	0.23	0.44	0.00									
6.Hokianga (*Bankia australis*)	0.27	0.27	0.24	0.39	0.3	0.006								
7. Mangonui (*B. australis*)	0.27	0.28	0.24	0.39	0.3	0.005	0.005							
8. Kaipara (*B. australis*)	0.27	0.28	0.25	0.39	0.3	0.006	0.006	0.005						
9.New Plymouth (*B. australis*)	0.27	0.27	0.24	0.39	0.3	0.007	0.006	0.006	0.002					
10.Whangarei (*B. australis*)	0.26	0.28	0.24	0.39	0.3	0.005	0.004	0.004	0.002	0.00				
11. Whangarei (*Lyrodus medilobatus*)	0.3	0.26	0.23	0.37	0.25	0.29	0.29	0.29	0.29	0.29	0.00			
12.Waitemata (*Lyrodus pedicellatus*)	0.32	0.25	0.24	0.38	0.25	0.28	0.28	0.28	0.28	0.28	0.21	0.01		
13.Tauranga (*L. pedicellatus*)	0.32	0.26	0.25	0.38	0.24	0.28	0.28	0.28	0.28	0.28	0.22	0.01	0.01	
14.Tauranga (Teredinidae sp.)	0.34	0.29	0.29	0.37	0.28	0.3	0.3	0.3	0.3	0.3	0.27	0.27	0.27	0.00

Discussion

The ability to reliably distinguish between native and non-native marine species is essential to enable conservation efforts and effective control measures, and several studies have proposed testable criteria outlining attributes to aid in the identification of introduced species (Chapman and Carlton 1991; Ruiz et al. 1997; Cranfield et al. 1998; Geller et al. 2010). For example, Cranfield et al. (1998) suggested nine criteria, based on those of Chapman and Carlton (1991), for determining introduced marine species in New Zealand, with criteria including species association with human mechanisms of dispersal or their prevalence on artificial environments. However, wood borers commonly associate with wood on marine infrastructures, and due to limited data to test the remaining criteria, questionable inferences of conservation status have resulted (Chapman and Carlton 1991; Ruiz et al. 1997; Cranfield et al. 1998; Geller et al. 2010).

Here we used a molecular approach (mitochondrial COI sequences) to further assess the status of marine wood borers in New Zealand. Specifically, our COI analyses provided support for a non-indigenous status of *Limnoria quadripunctata*. The limited diversity and low intraspecific divergence (0-1%) found among New Zealand *L. quadripunctata* populations suggests a likely introduction (*sensu* Chapman and Carlton 1991). Close genetic affinities to other geographic locations were found, with no divergences observed between populations from Napier and Chile (0.00%). The low divergence between Napier and Chile, and overall low diversity around New Zealand, suggests *L. quadripunctata* is a recent arrival. Populations of *L. quadripunctata* in Chile also displayed low genetic differentiation and a genetic signature for recent colonization (Haye et al. 2012). Collectively, *L. quadripunctata* results from New Zealand and Chile support its introduced status in both countries, and suggest introductions may have originated from similar source populations, likely a native European range, with *L. quadripunctata* transported in the hulls of wooden ships. Perhaps not expected of an introduced species, *Limnoria quadripunctata* showed patterns of genetic structuring among the major geographic regions, consistent with those previously found for native New Zealand species (Ross et al. 2009). However, the degree of population structuring was limited (1-2%) compared to that typical of native crustaceans (4.6-8.3%) = (e.g., Knox et al. 2011). This genetic structuring and the widespread distribution of *L. quadripunctata* may be explained by multiple introductions to different New Zealand ports, with the natural current systems maintaining genetic differences of the distinct populations introduced to each area. Overall, the low genetic differentiation found among New Zealand *L. quadripunctata* and its genetic affinity to populations in Chile supports its inferred non-indigenous status, with its widespread distribution and geographical structuring explained by the occurrence of multiple introductions. To further understand the introduced range, source populations and invasion patterns of *L. quadripunctata*, sequencing of native European *L. quadripunctata* is essential.

From the Sphaeromatidae family, *Sphaeroma quoianum* has previously been considered native by Davidson et al. (2008) and non-indigenous by Johns (2010). The low genetic diversity and structuring (0.002-0.003%) found among populations, and the limited geographical extent of collection of this species, provides further support for a non-indigenous status. Compared to the expected levels of intraspecific divergence (4.5-8.3%) associated with population genetic structuring of native crustaceans around New Zealand, it is clear *S. quoianum* presents no similar pattern (Ross et al. 2009; Knox et al. 2011). A sphaeromatid species collected in Tauranga did not morphologically or genetically correspond to any known New Zealand wood borer species. However, this taxon did resemble a widespread New Zealand non-boring species, *Exosphaeroma* cf. *obtusum* (Hurley and Jansen 1977), which is primarily associated with inorganic benthic substrates (Hurley and Jansen 1977). Accordingly, the individuals we collected may have been living secondarily in the existing burrows of the borer species.

Sequences from New Zealand *Lyrodus pedicellatus* (Teredinidae) had high intraspecific divergences (>20%) relative to other individuals of the "same" species sequenced in France, and evidence of population genetic structuring was found among New Zealand populations (divergences >1%). Intraspecific divergence levels found for *L. pedicellatus* were consistent with those of native molluscan species (0.3-2%) previously associated with geographical structuring around New Zealand (Goldstien et al. 2006). These results suggest a native status for this putatively non-indigenous species (*sensu* Chapman and Carlton 1991). The intraspecific divergences between Waitemata and Tauranga *L. pedicellatus* populations (1%) exceeded comparative values for the native *Bankia australis* (0-0.007%), further supporting a native status. *Lyrodus pedicellatus* has a tropical to temperate cosmopolitan distribution (McKoy 1980). However, there is a current paucity of available global sequences, and *L. pedicellatus* has also proven particularly difficult to identify. For example, *L. pedicellatus* was identified in Florida but later re-described as *L. floridanus* (Turner 1966), while *L. pedicellatus* in Turkey is morphologically similar to those in France, but revealed high intraspecific divergence (≥20%) (Borges et al. 2012). With such close morphological similarities in *Lyrodus* populations, it is possible that what is identified as *L. pedicellatus* in New Zealand may represent a different or undescribed species. Accordingly, Borges et al. (2012) suggested a reassessment of the New Zealand Teredinidae using a combined molecular and morphological approach would be beneficial.

Collectively, our findings suggest a need for further taxonomic analyses and support the idea that testable criteria such as those provided by Cranfield et al. (1998) present unsystematic bias (Hayden et al. 2009; Ruiz et al. 2000). In this case, past criteria overlooks the historical dispersal and unknown origins of New Zealand wood borers, and places too much weight on their preferred habitat. Future research collaboration and ongoing DNA barcoding of borer species in different regions would greatly assist in elucidating borer status', and thus the native diversity of different regions, ultimately improving our overall scientific understanding of marine species (Geller et al. 2010).

Verifying the status of marine wood borers is essential for future management and detection of potentially non-indigenous species. Biosecurity measures can only be undertaken if a species is considered a pest, illustrating the need for knowledge of a species native or non-indigenous status (Hayden et al. 2009). Furthermore, the maintenance of New Zealand's natural biodiversity is a significant issue (Hayden and Whyte 2003). If a non-indigenous species is truly native their ecologically important presence and role in woody debris decomposition should be protected.

We conclude that there is genetic support for the inferred non-indigenous status of *Limnoria quadripunctata*. The geographical structuring and genetic diversity of this species also drew attention to the possibility of multiple introductions, with New Zealand's distinct current systems maintaining genetic differences of introduced species. Such genetically divergent regions have been associated with native New Zealand species in the past; however, with the possibility of introductions from distinct populations to new locations, isolated by land and mixing patterns, geographical structuring may also signify the presence of non-indigenous species. We also suggest the native status of *Sphaeroma quoianum* requires further re-evaluation, while the inferred non-indigenous *Lyrodus pedicellatus* may in fact be native to New Zealand. The possibility of misidentified *Lyrodus pedicellatus*, and presence of an unidentified sphaeromatid wood borer, also highlights the patchy taxonomy and systematics surrounding marine wood borer species. Overall, COI sequences provided a beneficial tool in helping to elucidate the native or non-indigenous status of marine wood borers. Although being a global issue there is a clear requirement for ongoing DNA barcoding and international collaboration for future studies.

References

Ahyong ST, Wilkens SL (2011) Aliens in the Antipodes: non-indigenous marine crustaceans of New Zealand and Australia. In: Galil BS, Clarke PF, Carlton JT (Eds) In the wrong place- alien marine crustaceans: distribution, biology and impacts. Springer, New York, pp 451-485

Björdal CG, Gregory D, Manders M, Al-hamdani Z, Appelqvist C, Haverhand J, Dencker J (2012) Strategies for protection of wooden underwater cultural heritage in the Baltic Sea against marine wood borers. Conservation and Management of Archaeological Sites 14:201-214

Blakeslee AMH, Byers JE, Lesser MP (2008) Solving cryptogenic histories using host and parasite molecular genetics: the resolution of *Littorina littorea*'s North American origin. Molecular Ecology 17:3684-3696

Borges LMS, Sivrikaya H, le Roux A, Shipway JR, Cragg SM, Costa FO (2012) Investigating the taxonomy and systematics of marine wood borers (Bivalvia: Teredinidae) combining evidence from morphology, DNA barcodes and nuclear locus sequences. Invertebrate Systematics 26:572-582

Cannicii S, Burrows D, Fratini S, Smith III TJ, Offenberg J, Dahdouh-Guebas F (2008) Faunal impact on vegetation structure and ecosystem function in mangrove forests: a review. Aquatic Botany 89:186-200

Carlton JT (1987) Patterns of transoceanic marine biological invasions in the Pacific Ocean. Bulletin of Marine Science 77:1653-1655

Carlton JT, Geller JB (1993) Ecological roulette: The global transport of nonindigenous marine organisms. Science 261:78-82

Carlton JT (1996) Biological invasions and cryptogenic species. Ecology 77:1653-1655

Carlton JT (1999) The scale and ecological consequences of biological invasions in the World's oceans. In: Sandlund OT, Schei PJ, Viken A (Eds) Invasive species and biodiversity management. Kluwer Academic Publishers, Netherlands, pp 195-212

Chapman JW, Carlton JT (1991) A test of criteria for introduced species: the global invasion by the Isopod *Synidotea laevidorsalis* (Miers, 1881). Journal of Crustacean Biology 11:386-400

Cobb K (2002) Return of a castaway, the gripping story of a boring clam. Science News 162:72-74

Cookson LJ (1991) Australasian Species of Limnoriidae (Crustacea: Isopoda). Memoirs of the Museum of Victoria 52:137-262

Cragg SM, Pitman AJ, Henderson SM (1999) Developments in the understanding of marine wood boring crustaceans and in methods of controlling them. International Biodeterioration and Biodegradation 43:197-205

Cranfield HJ, Gordon DP, Willan RC, Marshall BA, Battershill CN, Francis MP, Nelson WA, Glasby CJ, Read GB (1998) Adventive marine species in New Zealand. NIWA Technical Report 34:5-35

Davidson TM (2008) Prevalence and distribution of the introduced burrowing Isopod, *Sphaeroma quoianum*, in the intertidal zone of a temperate Northeast Pacific Estuary (Isopoda: Falbillifera). Crustaceana 81:155-167

Distel DL, Amim M, Burgoyne A, Linton E, Mamangkey G, Morrill W, Nove J, Wood N, Yang J (2011) Molecular phylogeny of Pholadoidea Lamarck, 1809 supports a single origin for xylotrophy (wood feeding) and xylotrophic bacterial endosymbiosis in Bivalvia. Molecular Phylogenetics and Evolution 61:245-254

Drummond AJ, Rambaut A (2007) Bayesian evolutionary analysis by sampling trees. BMC Evolutionary Biology 7:214

Fofonoff PW, Ruiz GM, Steves B, Carlton JT (2003) In ships or on ships? Mechanisms of transfer and invasion for nonnative species to the Coasts of North America. In: Ruiz GM, Carlton JT (Eds) Invasive Species, Vectors and Management Strategies. Island Press, Washington, pp 152-182

Folmer O, Black M, Hoen W, Lutz R, Vrjenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit 1 from diverse metazoan invertebrates. Molecular Marine Biology and Biotechnology 3:294-299

Geller JB, Darling JA, Carlton JT (2010) Genetic Perspectives on Marine Biological Invasions. Annual Review of Marine Science 2:367-393

Goldstien SJ, Schiel DR, Gemmell NJ (2006) Comparative phylogeography of coastal limpets across a marine disjunction in New Zealand. Molecular Ecology 15:3259-3268

Guindon S, Gascuel O (2003). A simple, fast and accurate method to estimate large phylogenies by maximum-likelihood. Systematic Biology 52:697-704

Hayden BJ, Whyte CF (2003) Invasive species management in New Zealand. In: Ruiz GM, Carlton JT (eds) Invasive species vectors and management strategies. Island Press, Washington, pp 270-291

Hayden BJ, Inglis GJ, Schiel DR (2009) Marine invasions in New Zealand: a history of complex supply-side dynamics. In: Rilov G, Crooks JA (Eds) Biological invasions in marine ecosystems. Springer-Verlag, Berlin, pp 409-423

Haye PA, Varela AI, Thiel M (2012) Genetic signatures of rafting dispersal in algal-dwelling brooders *Limnoria* spp. (Isopoda) along the SE Pacific (Chile). Marine Ecology Progress Series 455:111-122

Hebert PDN, Ratnasingham S, deWaard JR (2003b) Barcoding animal life: cytochrome *c* oxidase subunit 1 divergences among closely related species. Proceedings of the Royal Society 270:S96-S99

Hickey JR, Lavery SD, Hannan DA, Baker SC, Clements KD (2009) New Zealand triplefin fishes (family Tripterygiidae): contrasting population structure and mtDNA within a marine species flock. Molecular Ecology 18:680-696

Hurley DE, Jansen KP (1977) The marine fauna of New Zealand: family Sphaeromatidae (Crustacea Isopoda: Flabellifera). Memoir New Zealand Oceanographic Institute 63:2-95

Ivanova N, Grainger C (2014) CCDB Protocols COI Amplification. http://ccdb.ca/docs/CCDB_Amplification.pdf. Accessed 12 December 2013

Johns PM (2010) New Zealand inventory of biodiversity: Phylum Arthropoda, Subphylum Crustacea, In: Gordon DP (ed) Volume 2 Kingdom Animalia. Canterbury University Press, Christchurch, pp 98-232

Kimura M (1980) A simple method for estimating evolutionary rate of base substitutions through comparative studies of nucleotide sequences. Journal of Molecular Evolution 16:111-120

Knox MA, Hogg ID, Pilditch CA (2011) The role of vicariance and dispersal on New Zealand's estuarine biodiversity: the case of *Paracorophium* (Crustacea: Amphipoda). Biological Journal of the Linnean Society 103:863-874

McKoy JL (1980) Distribution of shipworms (Bivalvia: Teredinidae) in the New Zealand region. New Zealand Journal of Marine and Freshwater Research 14:263-275

McQuire AJ (1964) A note on the occurrence of marine wood borers in New Zealand. Proceedings of the New Zealand Wood Preservers Association 4:35-44

Miller RC (1926) Ecological relations of marine wood-boring organisms in San Francisco Bay. Ecology 7:247-254

Messing J (1983) New M13 vectors for cloning. Methods in Enzymology 101:20-78

Minchin D, Gollasch S, Cohen AN, Hewitt CL, Olenin S (2009) Characterizing vectors of marine invasions. In: Rilov G, Crooks JA (eds) Biological invasions in marine ecosystems: ecological, management and geographic perspectives, Springer-Verlag, Berlin, pp 106-116

Paalvast P, van der Velde G (2011) Distribution, settlement, and growth of first-year individuals of the shipworm *Teredo navalis* L. (Bivalvia: Teredinidae) in the Port of Rotterdam area, the Netherlands. International Biodeterioration and Biodegradation 65:379-388

Pillai KN (1965) The role of crustacea in the destruction of submerged timber. Paper presented at the Symposium on Crustacea Part three, Ernakulam. http://eprints.cmfri.org.in/6799/. Accessed 16 December 2013

Posada D. In press. jModelTest: Phylogenetic model averaging. Molecular Biology and Evolution 25:1253-1256

Ratnasingham S, Hebert PDN (2007) The Barcode of Life Data System (http://www.barcodinglife.org). Molecular Ecology 7:355-364

Rimmer PJ (1967) The changing status of New Zealand seaports, 1853-1960. Annals of the Association of American Geographers 57:88-100

Ross PM, Hogg ID, Pilditch CA, Lundquist C J (2009) Phylogeography of New Zealand's coastal benthos. NZ Journal of Marine and Freshwater Research 43:1009-1027

Ross PM, Hogg ID, Pilditch CA, Lundquist CJ, Wilkins RJ (2012) Population genetic structure of the New Zealand estuarine clam *Austrovenus stutchburyi* (Bivalvia: Veneridae) reveals population subdivision and partial congruence with biogeographic boundaries. Estuaries and Coasts 35:143-154

Ruiz GM, Carlton JT, Grosholz ED, Hines AH (1997) Global invasions of marine and estuarine habitats by non-indigenous species: mechanisms, extents and consequences. American Zoologist 37:621-632

Ruiz GM, Fofonoff PW, Carlton JT, Wonham MJ, Hines AH (2000) Invasion of coastal marine communities in North America: apparent patterns, processes, and biases. Annual Review of Ecology and Systematics 31:481-531

Sakai AK, Allendorf FW, Holt JS, Lodge DM, Molofsky J, With KA, Baughman S, Cabin RJ, Cohen JE, Ellstrand NC, McCauley DE, O'Neil P, Parker IM, Thompson JN, Weller SG (2001) The population biology of invasive species. Annual Review of Ecology, Evolution, and Systematics 32:305-332

Santhakumaran LN (2003) Wood-borers. UNU-INWEH Course 1-International Training Course on Mangroves and Biodiversity. Centre of Advanced Studies in Marine Biology, Annamalai University, India, pp 425-437

Scotte M (1989) Two new species of wood-boring *Limnoria* (Crustacea: Isopoda) from New Zealand *L. hicksi* and *L. reniculus*. Proceedings of the Biological Society of Washington 102:716-725

Shears NT, Smith F, Babcock RC, Duffy CAJ, Villouta E (2008) Evaluation of biogeographic classification schemes for conservation planning: application to New Zealand's coastal environment. Conservation Biology 22:467-481

Simberloff D, Brown BJ, Lowrie S (1978) Isopod and insect root borers may benefit Florida mangroves. Science 18:630-632

Stevens MI, Hogg ID, Chapman MA (2002) The corophiid amphipods of Tauranga Harbour, New Zealand: evidence of an Australian crustacean invader. Hydrobiologia 474:147–154

Svarvarsson J, Osore MKW, Ólafsson E (2002) Does the wood-borer *Sphaeroma terebans* (Crustacea) shape the distribution of the mangrove *Rhizophora mucronata*? Ambrio 31:574-579

Swofford DL (2002) PAUP*. Phylogenetic analysis using parsimony, version 4.0b10 for Macintosh. Sinauer Associates Inc., Sunderland MA

Tamura K, Peterson D and N, Stecher G, Nei M, Kumar S (2011) MEGA5: Molecular Evolutionary Genetics Analysis Program for automated and iterative data analysis. Bioinformatics 28:2685-2686

Turner RD (1966) A survey and illustrated catalogue of the Teredinidae. Museum of Comparative Zoology Harvard University, Cambridge

Chapter IV

Thesis Summary and Conclusions

The historical nature of wood borer dispersal in the hulls of wooden ships around the world has left many species with uncertain origins and timing of introduction to different regions. The ability to reliably distinguish between native and non-native marine species is essential to facilitate conservation efforts and effective control measures (Ruiz et al. 1997; Geller et al. 2010). This thesis has addressed the limited biogeographical and historic data for New Zealand marine wood borers, to provide a greater understanding and awareness of the borer issues worldwide. New Zealand presented an ideal case-study with a significant history of borer issues and the presence of numerous wood borer species of both presumed native and non-indigenous status.

Chapter II highlighted the significant role of marine wood borers in environmental history by drawing attention to the largely unacknowledged social, economical and political impacts associated with borers, particularly in the period after 1800, which witnessed a massive growth in shipping networks (Manning 2005). Globally recognised for their destructive nature, the profound impacts were clear in the historic descriptions of sturdy seaworthy wooden ships and marine infrastructure reduced to honeycombed wrecks. Furthermore, the search for effective wood preservation to resist borers was, and still is, of concern. More specifically, the New Zealand setting provided a detailed record of the impacts and management of borers. Historical evidence in colonial newspapers, official statistics of New Zealand, and the detailed shipping movements by Rimmer (1966), proved invaluable in determining the pattern, distribution and management of borers across the entire country. Such evidence illustrated the growing awareness of borer destruction leading up to the twentieth century, corresponding with the significant growth in international shipping volumes after 1850. Furthermore, the historical evidence highlighted the repeated trial and error of borer management attempts, despite the occurrence of international and local scientific research. The amalgamation of literature on the historical persistence and impacts of borers, along with the many associated management attempts, provided a new perspective for marine invasive species and their role in environmental history.

In Chapter III, mitochondrial DNA (COI) sequences were used to further assess the inferred native and non-indigenous status of marine wood borers in New Zealand. Few of the past criteria used to determine this status were applicable to wood borers (Chapman and Carlton 1991; Cranfield et al. 1998). For example, Cranfield et al. (1998) suggested nine criteria based on Chapman and Carlton (1991), for determining introduced marine species in New Zealand, with criteria including species association with human mechanisms of dispersal or their prevalence on artificial environments. However, wood borers commonly associate with wood on marine infrastructures, and combined with the limited data to fulfil the remaining criteria, and their uncertain origins and timing of introduction, questionable inferences of their non-indigenous status were made (Chapman and Carlton 1991; Cranfield et al. 1998).

This study revealed low genetic diversity among *Limnoria quadripunctata* (Arthropoda; Isopoda) populations and close genetic affinity to Chilean populations supporting its inferred non-indigenous status, and suggesting recent arrival (Chapman and Carlton 1991; Cookson 1991). The population genetic structuring of *L. quadripunctata* showed a similar pattern to the genetically divergent regions previously identified for native New Zealand species (Ross et al. 2009). Although, *L. quadripunctata*'s lower levels of divergence in comparison to native crustaceans (e.g. Knox et al. 2011) suggests the occurrence of multiple introductions is more likely. Sequence data for *Sphaeroma quoianum*

(Arthropoda; Isopoda) also suggested a non-indigenous status, with low genetic diversity and no structuring among populations. By contrast, the inferred non-indigenous status for *Lyrodus pedicellatus* (Mollusca; Bivalvia) has been re-evaluated in the context of this study and I now suggest that it is likely to be native to New Zealand. The potential for a native status was based on high intraspecific divergences (>20%) between the same putative species in France, and evidence of population structuring in New Zealand, consistent with the degree of divergence previously described for native molluscs (e.g. Goldstien et al. 2006).

Taxonomic discrepancies were also revealed in this study. *Lyrodus pedicellatus* has proven difficult to identify in the past (Borges et al. 2012), and its high intraspecific divergence from populations in France suggests the *L. pedicellatus* identified in this study may present a different or undescribed species. The sphaeromatids in Tauranga Harbour had no morphological or genetic similarities to any other wood borers known in New Zealand, although presented similarities to another widespread sphaeromatid species, *Exosphaeroma* cf. *obtusum* (Hurley and Jansen 1977). Typically associated with benthic inorganic substrates these individuals may have been secondarily living in the burrows of other borer species.

Overall, the status of several borer species required re-evaluation, and *L. pedicellatus* presented the need for taxonomic revision. Past studies have been limited by the absence of historical data and may have used inappropriate criteria to determine borer status. Future research collaboration between historians and biologists, as well as ongoing DNA assessment of borer species, would assist in further elucidating native ranges and status', native or non-indigenous, in different biogeographical regions. Such information can influence whether the ecologically important role of native wood borers is protected, or management efforts are put in place to control the non-indigenous species.

Based on this research, I conclude that marine wood borers have played a significant role in marine environmental history, mediated largely by human transport and the provision of wooden habitats. The historical movement of wooden ships left many species' native or non-indigenous statuses difficult to determine. Mitochondrial DNA COI sequences provided a beneficial tool in elucidating the status of several New Zealand borers, effectively addressing the gaps in past criteria. There is a clear requirement for ongoing DNA barcoding and international collaboration to assist in future studies.

References

Borges LMS, Sivrikaya H, le Roux A, Shipway JR, Cragg SM, Costa FO (2012) Investigating the systematics of marine wood borers (Bivalvia: Teredinidae) combining evidence from morphology, DNA barcodes and nuclear locus sequences. Invertebrate Systematics 26:572-582

Chapman JW, Carlton JT (1991) A test of criteria for introduced species: the global invasion by the isopod *Synidotea laevidorsalis* (Miers, 1881). Journal of Crustacean Biology 11:386-400

Cranfield HJ, Gordon DP, Willan RC, Marshall BA, Battershill CN, Francis MP, Nelson WA, Glasby CJ, Read GB (1998) Adventive marine species in New Zealand. NIWA Technical Report 34:5-35

Cookson L J (1991) Australasian Species of Limnoriidae (Crustacea: Isopoda). Memoirs of the Museum of Victoria 52:137-262

Geller JB, Darling JA, Carlton JT (2010) Genetic Perspectives on Marine Biological Invasions. Annual Review of Marine Science 2:367-393

Goldstien SJ, Schiel DR, Gemmell NJ (2006) Comparative phylogeography of coastal limpets across a marine disjunction in New Zealand. Molecular Ecology 15:3259-3268

Knox MA, Hogg ID, Pilditch CA (2011) The role of vicariance and dispersal on New Zealand's estuarine biodiversity: the case of *Paracorophium* (Crustacea: Amphipoda). Biological Journal of the Linnean Society 103:863-874

Manning P (2005) Migration in world history. Routledge, New York, pp 132-156

Rimmer PJ (1967) The changing status of New Zealand seaports, 1853-1960. Annals of the Association of American Geographers 57:88-100

Ross PM, Hogg ID, Pilditch CA, Lundquist CJ (2009) Phylogeography of New Zealand's Coastal Benthos. NZ Journal of Marine and Freshwater Research 43:1009-1027

Ruiz GM, Carlton TJ (2003) Invasive species, vectors and management strategies. Island Press, Washington p ix